VI. *On the Structure and Affinities of* Matonia pectinata, R. Br., *with Notes on the Geological History of the Matonineæ.*

By A. C. Seward, F.R.S., *University Lecturer in Botany, Cambridge.*

Received February 28,—Read March 9, 1899.

[Plates 17-20.]

I.—Introduction.

In describing an ascent of Mount Ophir—about fifty miles east of Malacca, in the Malay Peninsula—Wallace writes as follows: "After passing a little tangled jungle and swampy thickets, we emerged into a fine lofty forest, pretty clear of undergrowth, and in which we could walk freely. We ascended steadily up a moderate slope for several miles, having a deep ravine on the left. We then had a level plateau or shoulder to cross, after which the ascent was steeper and the forest denser till we came out upon the "Padang-Batu," or stone-field, a place of which we had heard much, but could never get any one to describe intelligibly. We found it to be a steep slope of even rock, extending along the mountain side farther than we could see. Parts of it were quite bare, but where it was cracked and fissured there grew a most luxuriant vegetation, among which the pitcher plants were the most remarkable . . . . A few Coniferæ of the genus *Dacrydium* here first appeared, and in the thickets, just above the rocky surface, we walked through groves of those splendid ferns, *Dipteris Horsfieldii* and *Matonia pectinata*, which bear large spreading palmate fronds on slender stems, 6 or 8 feet high. The *Matonia* is the tallest and most elegant, and is known only from this mountain, and neither of them is yet introduced into our hot-houses." *

A sketch of *Dipteris* and *Matonia* accompanies this description. Both these ferns are of special interest on account of their rarity and isolation at the present day, and as living representatives of generic types which had a wide distribution in Europe during the Mesozoic epoch. The following pages deal with the structure of *Matonia pectinata* and with such records of fossil ferns as throw light on the past history of *Matonia* and closely allied genera.

---

* Wallace (86), p. 30. [The numbers in brackets after the author's name refer to the year of publication as given in the Bibliography at the end of the paper.]

The genus *Matonia* was defined in 1830 by ROBERT BROWN, and the diagnosis first appeared in WALLICH'S 'Plantæ Asiaticæ Rariores.' The choice of the generic name *Matonia* was in honour of Dr. W. G. MATON, F.R.S., Vice-President of the Linnean Society from 1774 to 1835. BROWN'S diagnosis is as follows:—

"Sori dorsales, rotundi, e puncto confluentiæ venularum plurium orti. Indusium orbiculatum peltatum. Capsulæ sessiles, in serie simplici circa receptaculum dispositæ."

"Filix pulcherrima lævis, fronde subbipinnata. Pinnæ plures hinc superiores, paucibus inde secundæ, omnes pinnatifidæ, lobis integerrimis singulis basi, nunc utroque latere, nunc inferiore tantum monosoris, raro bisoris." *

The type-specimen, on which the diagnosis of the genus and of the single species *Matonia pectinata* was founded, was collected by Colonel FARQUHAR in 1815, at an altitude of 4000 feet on Mount Ophir; it is now in the Wallich Herbarium, in the apartments of the Linnean Society, and the excellent drawing by C. M. CURTIS—the original of WALLICH'S plate—is in the collection of illustrations in the Kew Herbarium. On the sheet bearing the type-specimen WALLICH has written "*Prionopteris Farquhariana*, WALL. For *Prionopteris* substitute *Matonia pectinata*, BROWN." †

In 1842 Sir WILLIAM HOOKER gave an account of *Matonia pectinata* in HOOKER and BAUER'S 'Genera Filicum,' and published some new drawings of the specimen previously illustrated by WALLICH. He compares the sporangia with those of Cyatheaceous ferns.‡ The same author appended the following note to his description of the species in the 'Species Filicum': "Of late years I have received copious specimens of this magnificent and rare fern, and am satisfied that the genus belongs to the Cyatheaceous group." § In the 'Synopsis Filicum' *Matonia pectinata* is thus described: "One of the rarest and handsomest of ferns. Frond ample, fan-shaped, 1½ to 2 feet wide, hardly coriaceous. Each portion sub-scorpioideopinnate on one (the superior) side. Pinnules consequently all secund pectinato-pinnatifid." ||

MOORE refers *Matonia pectinata* to a special tribe, Matonineæ. "This remarkable and extremely handsome plant," he writes, "is quite unlike any other fern, and well deserves to rank as a distinct tribe, which we place in the neighbourhood of the Cyatheineæ, on account of the sub-oblique rings of the spore-cases."¶ BOMMER** follows MOORE, and places *Matonia* as the only genus in the tribe Matonineæ of the order Polypodiaceæ. JOHN SMITH, on the other hand, associates the genus with

---

* WALLICH (30), vol. 1, p. 16.

† *Vide* also BROWN (67), p. 531.

‡ HOOKER (42), London, 1867, p. 531.

§ HOOKER (64), p. 286.

|| HOOKER and BAUER (68), p. 45, Plate 1, fig. 8.

¶ MOORE (57), p. 106.

** BOMMER (67), p. 89, Plate 3, fig. 7.

Gleichenia, but refers to the presence of an indusium as a distinguishing feature.* BEDDOME gives a figure of *Matonia pectinata* in his 'Ferns of British India,' and includes the genus among the Cyatheaceæ.† In CHRIST's recent work on ferns, *Matonia* is placed in the Matoniaceæ, which, with the Gleicheniaceæ, constitute the sub-class Oligangia. The somewhat crude figures of *Matonia pectinata*, given by CHRIST, do not convey a very accurate impression of the characteristic features of this species.‡

Until 1888 *Matonia pectinata* remained the only known representative of ROBERT BROWN's genus, but in that year Mr. BAKER,§ of Kew, published an account of the external features of a new fern discovered by Mr. CHARLES HOSE at Niah, Sarawak, which he named *Matonia sarmentosa*. This species is particularly interesting as the habit differs considerably from that of *M. pectinata*, while the sori and sporangia agree closely with those of the older species. The type-specimen of *Matonia sarmentosa* is in the Kew Herbarium, and the species is also represented in the British Museum collection. An examination of the material on which BAKER's diagnosis was based affords ample evidence in support of the reference of the species to the genus *Matonia*. As the author of the species says, it has "precisely the fructification of *Matonia pectinata*, which is completely different in habit." BAKER concludes his account of the new species by expressing the opinion that *Matonia* ought clearly to form a tribe by itself, and should not be united with the Cyatheaceæ.||

The existing accounts of *Matonia* are confined to the form of the fronds. HOOKER described the rhizome of *Matonia pectinata* as "creeping,"¶ but no detailed description accompanies any of the references to the habit of the species.

The generally accepted view as to the affinities of the genus is that it occupies a position intermediate between Gleicheniaceæ and Cyatheaceæ, and "evidently represents an ancient type now in course of extinction."** It is interesting to find that the anatomy of the stem and other characters amply bear out the view, founded solely on external characters, that *Matonia* stands alone among existing ferns. In the early part of the present year (1898) my friend, Mr. R. SHELFORD, of Emmanuel College, Cambridge, the Curator of the Sarawak Museum, forwarded me some material of the fronds and rhizomes of *Matonia pectinata* collected at Matang, 3000 feet above sea-level. My hearty thanks are due to him for having obtained the necessary material and preserving it in a manner suitable for anatomical investigation. Mr. SHELFORD tells me that *Matonia pectinata* has been found in Borneo on the

---

* SMITH (75), p. 340.

† BEDDOME (68), p. 186, Plate 186.

‡ CHRIST (97), pp. 335, 336.

§ BAKER (88), p. 256.

|| BAKER (91), p. 191, Plate 14.

¶ HOOKER (64), vol. 5, p. 286.

** SOLMS-LAUBACH, Graf zu (91), p. 154.

mountains Santuborg and Matang. On the latter *Matonia* grows only at the top, 3500 to 3800 feet above sea-level, and is not plentiful. It is confined to old jungle, and never occurs in jungle that has been cut down and allowed to grow up again. It always grows in damp places, reaching a height of about 4 to 6 feet, with a rhizome which creeps along the ground just below or just above the surface. The occurrence of this species is recorded by BURCH* in the Karimatae Islands, where it was collected by the late Mr. TEYSMANN, and it has been found near Sarawak by BECCARI and Bishop HOZE. Among other localities from which *Matonia* has been recorded mention may be made of Mount Ophir, Perak, Karimum Islands (off Singapore), Malacca, Gemong, Amboyna, &c.

A. EXTERNAL FEATURES.

i. *The Stem.*

The rhizome, with an average diameter of about 7 millims., is thickly covered with brown multicellular hairs, which give it an appearance similar to the creeping stem of the Hare's foot fern.† It branches fairly frequently in an apparently dichotomous manner, and gives off petioles from its upper surface, while a few dark brown slender roots are attached to different parts of the stem, and are by no means confined to the lower surface. A striking feature of the rhizome is the occurrence of young and old fronds on the same branch, apparently without conformity to the usual acropetal order of succession. This peculiarity is clearly shown in the pieces of stem represented in Plate 1, figs. 1–2. The portion of stem seen in fig. 1 bears five leaf-stalks, *a* — *e*; the first occurs immediately behind the blunt hairy apex, and appears in the photograph as a slight protuberance, *a*; the second, *b*, is still very short and enclosed in a thick felt of brown hairs; the third petiole, *c*, has emerged from its protective envelope, and exhibits a circinately coiled tip turned towards the stem apex; at *d* there is the torn base of what was probably a mature frond, and at *e* the fifth petiole appears in a slightly less advanced stage than the third leaf-bud *c*. Beyond *e* there was a sixth frond, not included in the photograph, slightly longer than *b*. The distance between the leaf-stalks shown in fig. 1 is 3 centims., and the length of the rhizome 13 centims. The photograph in fig. 2 illustrates the juxtaposition of two young fronds of approximately the same stage of elongation; the same figure also shows a general tendency of the hairs to curve upwards towards the upper surface of the rhizome, presenting an appearance as if the felt of the stem had been brushed in an upward direction. This characteristic feature is illustrated also in thick transverse sections of the rhizome. The longest piece of rhizome received from Borneo measured 26 centims. in length,

---

* BURCH, W. (84), p. 90.

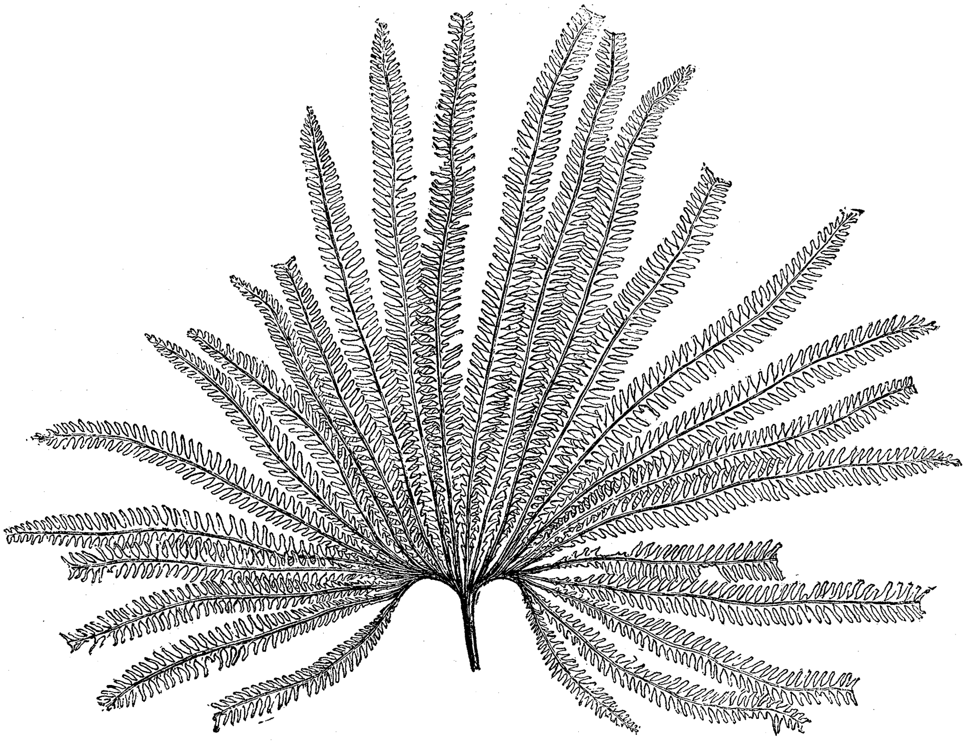
† A brief outline of the external features and anatomical structure of *Matonia pectinata* was given before Section K at the British Association at Bristol in 1898. [SEWARD (98).]

with one bifurcation, and bearing thirteen fronds in different stages of development. In one or two of the specimens of *Matonia pectinata* in the Kew and British Museum Herbaria, the frond is attached to a small piece of stem, but in most cases the leaf alone has been preserved by collectors. The apparent irregularity in the order of development of the leaves may be explained by assuming that only one frond matures on each branch of a rhizome; a somewhat similar manner of leaf-development may be seen on the rhizomes of species of *Davallia* and *Oleandra*.

ii. *The Leaf.*

The appearance of the fronds in their youngest form is shown in figs. 1 and 2, Plate 17, and fig. 30, Plate 19. An older frond presents the appearance of a closely coiled helix (fig. 3, Plate 17); the inner face of the leaf-stalk is slightly concave, and this enables the inner turns of the spire to be tightly embraced by the outer, the whole forming a compact and efficiently protected bud. In fig. 4 the crozier is partially unrolled, and the palmate pinnæ are just visible. In fig. 5 the unrolling has progressed rather further, and in fig. 6 the erect petiole is seen to be subdivided into several partially expanded hairy pinnæ, suggesting the characteristic habit of the mature frond. The form of the frond is seen more clearly in fig. 7; in this leaf the seventeen pinnæ are still slightly coiled at the apex, and the tips of the partially expanded pinnules are strongly revolute. The longest pinna has a length of 20 centims., and the largest pinnules are only 4 millims. long and 3 millims. wide. The accompanying sketch (text-figure 1), made from a specimen in the British Museum Herbarium, affords a good example of the characteristic habit of a mature frond; there are twenty-six pinnæ, the largest pinna being 44 centims. long, and the breadth of the whole leaf 61 centims., the long petiole branches to the right and left, giving off lateral members from the upper faces of its two recurved arms in a scorpioid manner. The axis of each pinna is winged in the basal portion, and the laminar border passes up gradually into the deeply pinnatified lamina, of which the ultimate linear segments are more or less falcate in form, tapering slightly to a blunt apex with a small median depression. The pinnules increase in size from the base of each pinna, and towards the middle reach a length of about 4 centims.; their margins are slightly revolute, especially near the blunt apex (figs. 13, 14, and 16, Plate 18); there is a well-marked midrib extending almost to the tip of each segment. The lateral veins are given off at a wide angle, and usually bifurcate close to their point of origin. Anastomoses between adjacent lateral veins are fairly common (fig. 23, A., Plate 18), especially near the midrib, where they give rise to areolæ not unlike the characteristic meshes on either side of the midrib in a pinnule of *Woodwardia*. The fairly regular radial series of areolæ in the upper part of the portion of lamina represented in fig. 23, B, *S*, marks the position of a sorus, the central plexus of vascular tissue being situated at the base of the receptacle which bore the sporangia. The frequent anastomoses of the veins seem to have been overlooked in previous descriptions; it is a fact of some importance in the comparison of recent and fossil species. HOOKER and BAUER refer to the recticulum below each sorus, but speak of the veins generally as free,[*] and a figure illustrating the venation in a recent work[†] in which the species is dealt with, represents the veins as free. In the two "nature prints" of *Matonia pectinata* in ETTINGSHAUSEN'S[‡] 'Farnkräuter der Jetztwelt' the veins are seen to be partially anastomosed. The venation may be described as a combination of the *Nervatio Tæniopteridis* and *N. Doodyæ.*[§]

Fig. 1.[||]



Matonia pectinata, R. BR. From a specimen in the British Museum Herbarium (one-fifth nat. size). Drawn by M. SEWARD.

The sori of *Matonia pectinata* have been described by several writers, one of the more recent accounts being by Professor ZEILLER[¶] in an important paper "Sur les Affinités du Genre *Laccopteris.*" The annulus is usually spoken of as complete and

---

[*] HOOKER and BAUER (68), p. 45.

[†] KRASSER (96), Plate 17, fig. 9.

[‡] ETTINGSHAUSEN, C. VON (65), Plate 155, fig. 11, and Plate 157, fig. 10.

[§] LUERSSEN (89), p. 12, figs. 7 and 19.

[||] My thanks are due to the University Press for the loan of this process-block.

[¶] ZEILLER (85.)

oblique, but an examination of several sporangia has convinced me that the annulus is incomplete, the well-defined dark-walled cells never extending completely round the sporangium (figs. 18-20, Plate 18). One striking feature as regards the occurrence of the sori is that all fronds appear to be fertile, and practically every pinnule bears one or more groups of sporangia. In fig. 7, Plate 17, most of the short segments are seen to bear two sori, which appear as slight circular projections near the base of each pinnule; in many of these young segments there are other sori nearer the apex of the lamina, which are hidden by the strongly recurved tips of the pinnules (fig. 13, Plate 18). In most cases the sori on each pinnule are few in number, frequently only one sorus on each segment, and this occurs on the lower side of the midrib close to the base. There may be as many as seven sori on a segment on the same side of the midrib, but usually the number is less, and the sporangial groups occur at irregular intervals on the lower face of the lamina, either above or below the mid-rib (fig. 14, Plate 18).

The sori are circular in form, approximately 9 millims. in diameter, and consist of 5-11 large sporangia sessile on a central columnar receptacle, which spreads out into an umbrella-shaped indusium, with its incurved margin tucked in below the ring of sporangia (fig. 17, Plate 18; fig. 41, Plate 20). When the sporangia are ripe the indusium is detached, leaving a projecting stump of the circular receptacle. The whole indusiate sorus is readily separated from its pinnule by the insertion of a needle, leaving a slight circular depression on the lamina with the remains of the receptacle as a button-like projection (fig. 14, Plate 18). These details are of some importance from the point of view of the comparison of recent and fossil fronds, especially as illustrating the difficulty of deciding whether a naked fossil sorus was originally indusiate. The annulus consists of prominent brown-walled cells, and is oblique and incomplete; each sporangium contains about 64 tetrahedral spores.

Fig. 20, Plate 18, represents a surface view of a sorus of eight sporangia, arranged round the basal stump to which the indusium was originally attached, and in fig. 19 two sporangia are seen edgewise; in both these drawings the oblique nature of the annulus is clearly demonstrated. In fig. 18 we have two views of the same sporangium; in fig. 18, A, the cells of the annulus are seen to extend to the narrow end of the sporangium, but after passing obliquely over the crest the annulus is continued for a short distance only down the opposite side, as shown in fig. 18, B.

B. Internal Structure.

a. *Rhizome.*

The appearance presented by a transverse section of the rhizome may be either as represented in fig. 8, Plate 17, or in fig. 9; in the former section the vascular tissue occurs in the form of two annular steles separated from one another by parenchymatous ground-tissue, the centre of the stem being occupied by parenchyma ; in the latter section the axial ground tissue is replaced by a strand of xylem surrounded by a band of phloem tissue. Both types of structure (figs. 8 and 9) are frequently met with in examining different portions of a stem, and one or other type represents the characteristic structural arrangement in the rhizome of *Matonia pectinata*.*

The peripheral portion of the stem consists of a band of dark-brown elongated "bast"† cells, without intercellular spaces, and with simple pits in the walls and occasional transverse septa. The outermost cells have somewhat thinner walls, and pass outwards into long multi-cellular hairs, which cover the rhizome with a dense brown felt. In several of the stem sections the peripheral tissue was found to have been partially destroyed by a fungus, hyphæ being abundant in the cell cavities.

Towards the interior of the stem the peripheral strengthening tissue passes into ordinary parenchyma. Each of the two annular gamosteles consists of a central ring of xylem surrounded by a band of phloem, and enclosed by an external and internal pericycle and endodermis. The endodermal layer is easily identified by the regular form of the cells, which have thinner walls than the neighbouring ground-tissue elements; the radial walls are slightly brown in colour, and easily torn in the process of cutting sections of the stem (*e.*, fig. 10, Plate 17). The pericycle consists of a single layer of cells, followed by narrow protophloem elements (*pt.*, figs. 10, 24, and 37), beyond which there are two or three rows of large sieve-tubes, with oblique ends and numerous sieve-plates on their lateral walls (*s.*, figs. 10, 24, and 37). The scalariform tracheids of the xylem have small groups of parenchyma associated with them, as seen in figs. 10, 24, 28, 34, and 37 ; the parenchymatous tissue stands out conspicuously as a deeply stained irregular reticulum in the section through the apical region of a rhizome, shown in fig. 28, Plate 19. The inner margin of the outer stele is characterised by a regular crenulate form (figs. 8, 9, 11, and 37), and in each bay there is a well-defined group of protoxylem tracheids. The structure of the outer stele and the position of three protoxylem groups, *px.*, are clearly shown in the photograph, fig. 37, Plate 20. In the comparatively small outer stele in fig. 8, Plate 17, there are ten protoxylem groups, while the larger vascular ring of fig. 9 has sixteen initial strands. The inner annular stele (figs. 8, 9, 10), agrees with the outer in being enclosed internally and externally by a pericycle and endodermis, but the xylem is rather broader, and the inner margin has not the crenulated form characteristic of the larger stele. There is a single group of protoxylem in the inner stele (*px.*, figs. 10, 24, 28), but this is not always very distinct in sections of the older portions of a rhizome. In transverse sections of the rhizome near the apical region, where the elements are not fully developed, the protoxylem is easily recognised (Plate 19, fig. 28, *px.*) as a small group of two or three thick-walled tracheids, slightly to one side of the

---

* I am indebted to my friend, Mr. PEARSON, of Caius College, for assistance in the preparation of sections.

† The term "bast" is here used in the old sense, as employed by HABERLANDT in his 'Physiologische Pflanzenanatomie.'

long axis of the stele, as seen in a transverse section. The shape of the inner stele varies in different regions of the stem; between the leaves it has the form of a circular or oval band (figs. 8–10), but near the point of origin of a leaf the continuity of the cylinder is broken (figs. 11 and 12, Plate 17), and in the immediate neighbourhood of a leaf the form may be as represented in fig. 24, Plate 19. The latter figure shows very clearly the structure of the stele, the large sieve-tubes (*s.*), the narrow and darker external phloem elements (*pt.*), the pericycle and endodermis (*e.*), and the xylem parenchyma.

The axial region of the stem, as seen in figs. 8 and 10, is occupied by thick-walled parenchymatous cells, with small intercellular spaces, but in the stem section, as shown in figs. 9, 11, 12, and 24, there is a strand of solid vascular tissue of concentric structure, constituting a third stele enclosed by a pericycle and endodermis. The size of this central stele varies considerably; it is unusually large in fig. 9, and in fig. 12 the number of tracheids is considerably less.

The structure of the axial stele is more clearly shown in fig. 34, Plate 20; the tissues agree with those in the annular steles, and there are a few xylem parenchymatous cells between some of the tracheids as in the other steles (the dark cells in fig. 28, Plate 19). No protoxylem elements have been recognised in the axial vascular strand.

The anatomy of the stem apex has not been completely made out, two apices having been sacrificed in unsuccessful attempts to obtain a series of microtome sections. In the diagrammatic sketch shown in fig. 39, Plate 20, which represents an approximately median section, the blunt growing-point is seen to have a broadly depressed apex, with a leaf-bud immediately behind it appearing as a slight protuberance at P. In this section the three steles extend to the apical region, and appear to be merged in a common meristem. The largest stele splits close to its origin into two annular steles and a central strand remains undivided as a small downward prolongation of the inner annular stele. The leaf-bud close to the apex (P, fig. 39) is supplied by the outer and in part by the inner annular stele.

In the apical region of the stem, the multicellular hairs consist of thin-walled cells, with large and conspicuous nuclei; in slightly older hairs the basal region consists of a few thin-walled living cells (*m*, fig. 32, Plate 19), while the greater portion of each hair is composed of a few long and narrow dead cells with brown walls (fig. 32).

The photograph reproduced in fig. 29, Plate 19, shows the appearance of an approximately median section through the apex of a stout rhizome. The short asymmetrical cone occupying the middle of the apical depression consists apparently of two or three large cells, but it is impossible to speak with certainty as to the existence of one single apical cell or of more than one initial element; in all probability, however, there is a single three-sided apical cell. This point can only be determined by a serial examination of microtome sections, for which material is not at present available. By a succession of radial walls, narrow segments are cut off parallel to the inclined sides of an apical cell;[*] these are followed by tangential walls which determine the limits of the stelar and extra-stelar tissues; in the procambium strands numerous narrow elements are cut off from the meristem cells by a succession of tangential walls, as shown in the right-hand arm of the outer stele. The disposition of the cell-walls in the apical meristem appears to agree with the development in gamostelic polystelic stems, as described by VAN TIEGHEM.[†] From the common apical meristem the two annular steles and the axial strand are gradually differentiated; the xylem parenchyma standing out prominently as dark cell-rows a short distance behind the apex. A figure of the apex of *Pteris aquilina,* given by HOFMEISTER,[‡] bears a fairly close resemblance to fig. 29; the summit of the stem has the same blunt form with a median depression.

Fig. 36 represents the stelar tissue, as seen in a transverse section just behind the stem apex; the outer stele presents the appearance of having been pulled towards one side where it is narrower, and a similar outward extension is seen in the second stele; the axial strand of xylem and phloem (iii) is here seen to be in direct connection with the second stele. The asymmetrical form of the annular steles is due to the presence of a leaf-bud immediately behind the apex.

In the regions *a, a* of the steles i and ii the tissue consists of parenchymatous meristem in which the elements are not yet differentiated; it is this portion which is extending outwards to form the vascular system of a leaf-bud. The xylem parenchyma stands out conspicuously, as anastomosing deeply stained rows of cells, throughout the greater portion of both steles. In the transverse section of the second stele and the axial vascular strand shown in fig. 28, Plate 19, the deeply stained xylem parenchyma is very conspicuous; sections cut near the apical region of a rhizome, as in fig. 28, illustrate very clearly the connected tissue-system formed by the parenchyma (amylom) which traverses the xylem.

The transverse section diagrammatically represented in fig. 38, Plate 20, was cut as near to the apex of the stem as possible; the triangular arrangement of the cells in the centre suggests the presence of the usual form of apical cell, and to one side of the apex a few of the young filamentous hairs are seen at *h, h.*

We may hope to obtain valuable evidence as to the origin of the mature stelar structure of *Matonia* when young plants are available for investigation. The study of the apical region as a guide to phylogeny is of little importance,[§] and we can only hazard a guess as to the development of the steles from a simpler type of stem; it is probable that after the formation of a single annular stele in the young plant the ring

---

[*] KLEIN, L. (84). KLEIN concludes that all dorsiventral fern stems, except *Pteris aquilina*, possess a single three-sided apical cell, as appears to be the case in *Matonia* [*cf.* Plate 20, fig. 38; *vide* also BOWER (89) pp. 318, *et seq.*]

[†] VAN TIEGHEM (91), pp. 773, 774.

[‡] HOFMEISTER (63), Plates 30 and 31.

[§] *Cf.* SCOTT (94), p. 472.

divided, and split off a second cylinder; but it is reasonable to hope that young plants may be obtained which will afford important data from the point of view of stelar evolution, not only in *Matonia*, but as regards the phylogeny of the *Matonia* type from a primitive axial stele.

b. *Root.*

In transverse sections of the stem, roots are frequently met with in different stages of development as slight protuberances on the edge of the outer annular stele (fig. 9, fig. 11, R), or as slender vascular strands enclosed in a sclerenchymatous sheath passing in a slightly oblique radial direction through the cortex of the stem (fig. 9). Two very young roots are shown in the diagrammatic section of the stem apex, represented in fig. 39, R i., and R ii.

The stele of the root is triarch, and the cortex consists of a few thin-walled cells enclosed in a dark brown band of schlerenchyma; in the outer layers of sclerous elements the cell lumina are almost obliterated by the thickening of the walls (fig. 42, Plate 20). In some sections of roots traces of thin-walled cells are seen external to the brown sclerous sheath; these are, no doubt, remnants of a piliferous layer. The roots always arise from the outer annular stele at points immediately opposite a protoxylem group; but they appear to be developed equally on all sides of the stele, if, indeed, they are not more numerous on the upper than on the lower side of the stele. The number of roots is small, but they are more abundant in the immediate neighbourhood of a leaf.

In tangential sections of the rhizome, outgoing roots are occasionally met with in slightly oblique transverse section, surrounded by three or four layers of dark brown sclerous cells.

c. *Leaf.*

Part of a transverse section of a pinnule is shown in fig. 26; the most striking feature is the peculiar form of the lower epidermal cells: they have thick outer walls, which are bulged outwards in the form of irregular rounded knobs. These peculiar cells appear as small crystal-like globules when the under surface of a leaf-segment is examined through a low-power lens. The upper epidermis consists of a regular row of cells with comparatively thick outer walls; the mesophyll is made up of a loose tissue in which the intercellular spaces are much larger towards the lower surface of the leaf, but there is no regular palisade arrangement.

The surface of the parenchymatous cells in the spongy mesophyll next the lower epidermis is studded with numerous minute rods (fig. 27, Plate 19), such as characterise the leaf-tissue of the Marattiaceæ, and some other ferns. These delicate outgrowths were originally described by LUERSSEN* as cuticular threads, but more recent writers,

---

* LUERSSEN (73).

MANGIN, HÖHNEL,* and others, regard them as pectin products of the middle lamella. POIRAULT† mentions these "bâtonnets intercellulaires" as being unusually developed in *Matonia pectinata*.

The stomata are confined to the lower surface, the guard-cells being on a level with the inner wall of the epidermal cells (figs. 26 and 27, Plate 19). Fig. 21, *a*, represents a surface view of a stoma in which the outer portions of the surrounding epidermal cells are in focus; in *b* the same group of cells is seen at a lower level, with the guard-cells in focus. The form of the epidermal cells is more clearly seen in fig. 22, drawn from the epidermis of a young leaf; the initial cell of a stoma is cut off by a curved wall from an epidermal cell, and this forms the stoma mother-cell.

The veins consist of a very few tracheids, and some at least appear to be collateral in structure; they are enclosed in a ring of fairly thick-walled cells, and each vein is succeeded above and below by two or three mechanical elements forming a simple type of I-shaped girder, stretching across the mesophyll of the leaf (fig. 26, Plate 19). There is scarcely any phloem in the smaller veins, but each is surrounded by a ring of fairly large parenchymatous cells. The margins of the pinnules are strengthened by a strand of thick-walled fibres. The chief point of interest in the structure of the midrib is the presence of an arc of fibrous elements in the lower portion of the phloem region, as seen in transverse section, next the xylem parenchyma; a single group of fibres also occurs in the middle of the upper portion of the midrib.

In a transverse section of a partially expanded pinnule, the edges of the lamina are seen to be strongly recurved (figs. 15 and 16), reminding one of the numerous Alethopteroid segments met with in the calcareous nodules of the Lower Coal seams. A more highly magnified portion of a young pinnule is shown in fig. 15, B; the cells of the upper epidermis (*Ep.*) form a conspicuous layer of radially elongated elements considerably larger at this stage than the epidermal cells of the lower surface. The axis of the pinna is traversed by a broad V-shaped stele, from which the lateral veins are given off on either side (figs. 15, A, and 16, Plate 18). Fig. 40, Plate 20, represents a vertical section through the tip of a young pinnule; the growing apex is occupied by a large dome-shaped cell.

The appearance of the sori in a somewhat older pinnule is diagrammatically represented in fig. 16; the indusium margin, which consists of a large-celled epidermis, is tightly tucked in underneath the young sporangia, and a group of short tracheids occurs (figs. 16 and 17) at the base of the columnar receptacle. The sporangia of a sorus are always found to be approximately of the same size, and there is not the association of young and old sporangia which characterises the polypodiaceous sorus‡ (figs. 13 and 17).

---

* HÖHNEL, F. VON (77), p. 507.

† POIRAULT (94).

‡ Some young sori have been placed in the hands of Professor BOWER, who informs me that a study of the development of the sporangia reveals nothing of any special interest; but an account of the early stages in the growth of the sorus will be given in a forthcoming memoir by Professor BOWER.

The individual sporangia appear to be attached to the short receptacle by about two cells. The spores are tetrahedral in shape, and show distinctly the usual three-rayed marking on the surface; they possess a thick exine, enclosing food granules of various size. The appearance of the spore-contents presents a striking resemblance to the thin vesicular bodies frequently met with in fossil macrospores, which have been described as prothalloid cells; it is not improbable that, in some cases, these so-called cells in the interior of fossil spores should be regarded as swollen cell-contents. The spores have a diameter of approximately ·07 millim.; the sporangia are about ·5 millim. long and ·33 millim. broad, rather larger than those of *Osmunda regalis*, L., species of *Todea* and *Gleichenia*, agreeing more closely in size with those of *Mohria Caffrorum*, DASV., and *Schizæa pusilla*, PURSH.

The structure of the petiole need not be described in detail. Fig. 31 illustrates the general arrangement of the hypoderm, ground-tissue and stelar-tissue; the flattened appearance of some of the ground-tissue of this section is due to a transverse shrinking of the petiole. The stele has the form of a broad U-shaped band, with the ends of the two arms bent inwards in an almost horizontal direction, with the tips bent downwards and outwards as shown in the photograph. The inner margin of the stele is crenulate as in the outer annular stele of the stem, and each "bay" is occupied by a group of protoxylem elements. There are usually about thirty groups of spiral tracheids in the stele of a petiole. A portion of the stele is more clearly shown in fig. 25, Plate 19; the endodermis and pericycle are identical with those of the stem, but there is a distinct strand of loose parenchyma in contact with each group of spiral tracheids. The occurrence of these loose parenchymatous strands next the protoxylem groups of ferns has often been referred to by different writers. RUSSOW* proposed the term "Lückenparenchym" for the parenchymatous cells filling the space produced by the tearing of the tissues near the protoxylem, and TERLETZKI† refers to the same tissue as "Stumpfzellen-Stränge" in *Pteris aquilina*, L., *Osmunda*, and *Cyathea medullaris*, Sw.

At F in fig. 25 the bend of the stelar band is occupied by a group of strong stereome elements, which occur in the phloem region, and a few larger thick-walled cells are found in the ground-tissue just above the endodermis (fig. 25, *Sl.*, Plate 19). In the angle of the sharp bend of the petiole stele (*x.*, fig. 31) there is another band of fibres abutting on the xylem parenchyma.

In fig. 30, A, Plate 19, a young petiole is shown in side view, the base is enclosed in a mass of the rhizome hairs, and similar hairs are attached to the concave inner face below the overhanging apex of the frond. A front view of the same frond is represented in fig. 30, B, and at C and D diagrammatic sections through the regions

---

* RUSSOW (72), p. 101.

† TERLETZKI (84), pp. 463, 494, Plate 25, fig. 10. *Vide* DE BARY (84), p. 346, who mentions the occurrence of Lückenparenchym in species of *Asplenium*, as well as in other genera; also STRASBURGER (91), p. 444.

indicated by *ab*, *cd* in fig. B. Section C shows the tip of the frond clasped by the edges of the grooved surface of the leaf-stalk, and in section D the face of the groove is seen to be clothed with hairs. In both sections, C and D, the shaded portion of the drawing between the stele and the edge of the leaf marks the position of meristematic tissue in an active state of growth.

In cutting a series of transverse sections through the tip of a young frond like that in fig. 30, Plate 19, we first meet with indications of the stele in the form of regular meristematic cell-rows occupying the centre of the apical region; passing further down a few thin-walled tracheal elements appear in the form of a crenulate group, foreshadowing the characteristic outline of the mature stele; on the posterior side of the frond axis, at a slightly lower level, the undifferentiated meristem forms an elliptical ring of tissue with a stout band of tracheids on the posterior side. At a still lower level the anterior margin of the meristem band curves inwards in the form of two arms representing the first appearance of the incurved bands of fig. 30, C, which gradually pass over into the revolute ends of the stelar band.

Fig. 2.

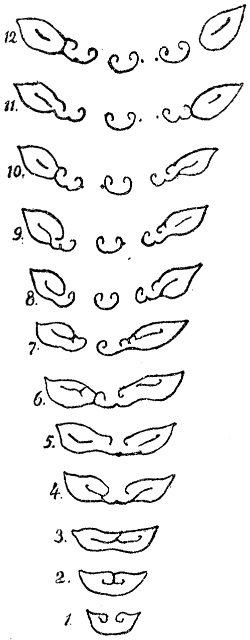


Diagram illustrating the division of the single petiolar stele into the vascular strands of the pinnæ.

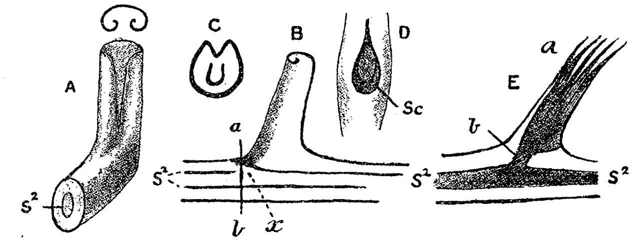
In the text-figure 2, a series of drawings is reproduced of a succession of transverse sections of the stelar tissues of a leaf-stalk, representing the gradual alteration in the shape of the stele in the region near the tip of the petiole, just below the point at which it breaks up into the numerous pinnæ.

The petiole stele gradually widens, and alters in shape until a separate U-shaped branch becomes detached (8). A second branch is afterwards given off, as seen in section 12, which was cut just below the level at which the pinnæ become free, and a third is nearly ready to be separated off on the left-hand side of the same section.

d. Origin of the Leaf-trace, and behaviour of the Steles in the region of Branching.

The connection between the stele of a leaf-stalk and those of the rhizome is illustrated by a series of diagrams reproduced in the text-figures 3–5. Fig. 3, A, represents a surface view of the outer annular stele of the stem, after the removal of the extra-stelar tissues, passing upwards into the petiole; a gap is formed in the stele on the anterior side of the leaf-stalk, and the edges of the gap are bent inwards to form the characteristic incurved ends of the foliar stele.

Fig. 3.



Sketches illustrating the origin of the petiolar stele.
S^2, second (inner) annular stele of the rhizome; S*c*, scar on the edge of the gap of the inner stele (S^2) to which the ascending branch (*b*, fig. E) was attached.

At B the piece of stem is shown in median section; the erect branch of the outer stele is seen to be continuous with the inner annular stele (S_2), the continuity of the inner stele being interrupted by a short gap (*x*), a point below that at which the outer stele bends up into the petiole. In a transverse section through the rhizome immediately in front of the petiole base, the two steles present the appearance shown in C, which was cut along the line *ab* of fig. 3, B; the outer stele is deeply grooved on the upper surface, and the inner stele has the form of a U.

A surface view of the inner annular stele (fig. 3, D), after the removal of the outer stele, shows the gap made by the passing upwards of a portion of the stele which contributes to the formation of the meristele of the leaf. The curved scar, Sc, on the edge of the gap marks the place where the upward branch was cut off in the process of dissecting the rhizome. Fig. 3, E, represents the second annular stele in side-view, with the ascending branch, *b*, joining on to the outer vascular ring to form the incurved edges of the petiole stele. The ribbed appearance in the upper portion of the petiole (*a* fig. 3, E), is due to the crenulated inner edge of the stele; this dissection demonstrates the small share taken by the inner stele of the rhizome in supplying the vascular system of the leaf.

Fig. 4, *α*, represents a series of diagrammatic sections of the stelar tissue, transverse to the petiole and longitudinal to the stem; the incurved ends of the petiole stele are found to gradually unite, and finally pass downwards as a slightly curved band to unite with the inner stele of the rhizome. The form of this downward branch, as seen at *b* in section 4, corresponds with the curved scar, S*c*, of fig. 3, D, on the edge of the gap in the inner annular stele.

Fig. 4.

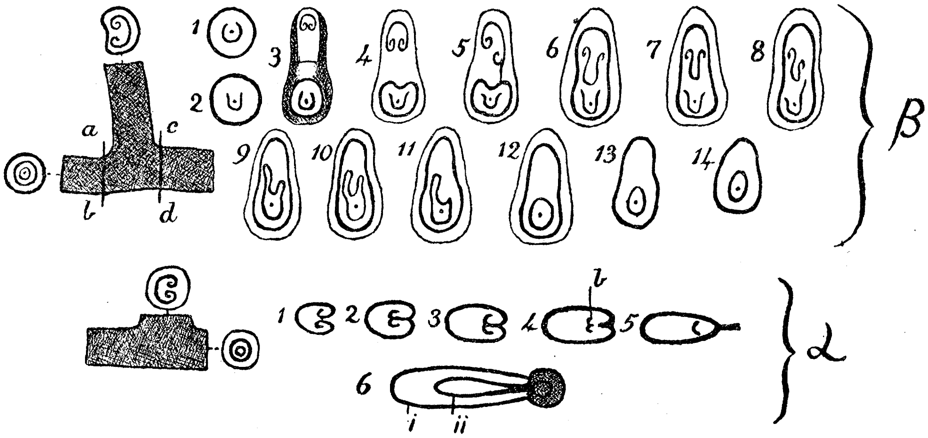


Diagram illustrating the origin of the petiolar vascular system from the rhizome steles.
α.—A series of longitudinal sections through the rhizome; *β.*—A series of transverse sections through the rhizome in the nodal region. i. and ii. in fig. 6, *α*, denote the outer and inner steles of the rhizome.

The diagrams in fig. 4, *β*, illustrate the behaviour of the rhizome steles in passing through a nodal region; a transverse section through the rhizome at *ab*, immediately in front of the leaf, shows the outer annular stele almost circular in outline, and the inner annular stele in the form of a U (section 1); in section 2 the inner stele is more widely open, and the outer stele is arched slightly upwards. The third axial stele, which is present in this piece of stem, passes through the node without participating in the vascular supply of the leaf. Sections 3 to 14 show the gradual arching upwards of the outer stele into the petiole, the passing downwards of the foliar stele into the second annular stele of the rhizome and the closing of the foliar gap in the latter.

The photographs 11 and 12, Plate 17, represent the appearance of the steles in a transverse section of the rhizome immediately in front of a leaf.

It may happen that the third stele of the rhizome becomes directly connected with the inner annular stele in the nodal region; this is shown in the diagrams of sections in text-figure 5 and in the larger diagram, fig. 35, Plate 20. Similarly, in fig. 36, Plate 20, the second and third steles are in direct continuity. In section 1, fig. 5, taken just in front of a leaf-bud, the axial stele appears as an inward prolongation of the second annular stele; as the annular stele opens, the connection is maintained (section 2), but immediately behind the leaf the axial stele becomes free (section 5).

It would appear, then, that the third vascular strand may arise as an offshoot from the second annular stele near the point of origin of a leaf (*cf.* fig. 36, Plate 20).

The photograph reproduced in fig. 24, Plate 19, shows the inner stele, and a small axial stele as seen in a transverse section of the stem just behind a leaf; the two broader portions of the vascular cylinder projecting into the internal ground-tissue may be regarded as the "roots" or bases of the branch which connects the second annular stele and the incurved edges of the leaf-trace.

Fig. 5.

Diagrams showing the connection between the axial stele of the rhizome and the vascular system of a leaf.

The behaviour of the rhizome steles in the region of branching is illustrated in text, fig. 6. Section 1 shows the rhizome cut through along the line *ab*; three steles (S^1, S^2, S^3) are present. In the sections 2–16 the steles only are drawn in outline. The chief points of interest are the gradual flattening, constriction, and final splitting, first of the inner, and afterwards of the outer annular stele; also the absorption of the axial stele into the widening second annular stele. Section 17 shows the rhizome in

Fig. 6.

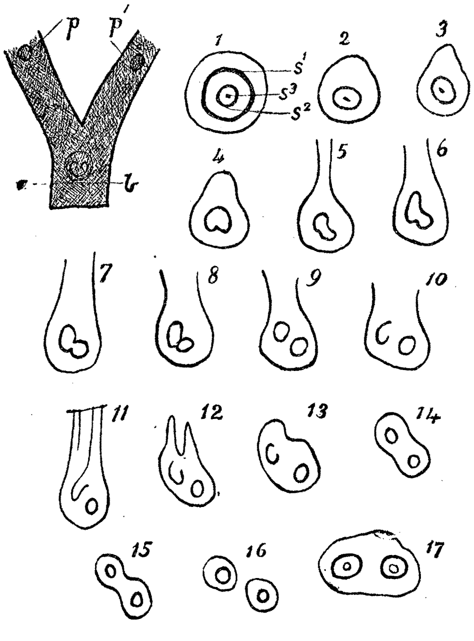


Diagram illustrating the behaviour of the rhizome stele in the region of branching.

transverse section, including two pairs of steles, immediately in front of the bifurcation. This bifurcation of the steles may be compared with a similar behaviour of stelar tissue in forking *Lepidodendron* stems.

In a few cases the axial stele has been found to die out gradually without becoming connected with the second stele. Twenty-two transverse sections were cut as close together as possible, in order to follow the axial stele to its termination. In section 1 the stele contained 10 tracheids; in section 9 about 7, and some of these were filled with a brown substance; in section 12 a single tracheid remained, its cavity being filled with some brown material, probably a product of degradation; beyond this point the stele consisted exclusively of sieve-tubes and parenchyma (as shown in fig. 33, Plate 20), and finally nothing remained but a small strand of delicate cells embedded in the thick-walled ground-tissue, and associated at its periphery with a few reticulately thickened isodiametric elements. The existence of the brown degradation product in some of the last tracheids is, no doubt, a pathological result of the loss of function of this blindly ending vascular strand.

C. COMPARISON OF MATONIA PECTINATA WITH OTHER FERNS.

α. *Stem.*

The most striking anatomical feature in the rhizome of *Matonia pectinata* is the annular character of the stelar tissue, and the occurrence in some portions of the stem of a solid axial strand of xylem and phloem. Although the published figures of fern stems in text-books have not made us familiar with the existence of an annular form of stele similar to that in *Marsilia*, it has long been known that this type of gamostely is by no means uncommon among ferns of different families. In a short account of a rare Javan fern, *Polypodium* (*Dipteris*) *Horsfieldii*, R. BR., written in 1838, ROBERT BROWN* describes the stem as possessing "a complete circle of *Vasa Scalariformia* separating the ligneous or fibrous vessels of the caudex into an outer cortex and inner portion." This structure, he adds, while not peculiar to *Dipteris*, seems to be of rare occurrence among ferns; it exists also in the "Caudex of *Platyzoma* and *Anemia*." VON MOHL,† in 1845, quotes BROWN's reference to the closed ring of vessels in these three genera. METTENIUS, one of the best among botanical anatomists, in two papers published in 1864 and 1865, refers to a closed "vascular bundle" in *Loxsoma*,‡ and in another place he deals at some length with the annular steles and the medullary vascular strands in other ferns.

METTENIUS points out that KARSTEN investigated the structure of *Dicksonia* (*Dennstædia*) *rubiginosa*, KAULF., *Pteris orizatæ*, *P. gigantea*, WILLD., and *Sacco*-

---

* BROWN, R., in HORSFIELD (38), pp. 1 and 2 [*P. Horsfieldii*, R. BR. = *P. Dipteris*, BLUME; HOOKER and BAKER (68), p. 362].

† VON MOHL (45).

‡ METTENIUS (65), p. 418.

loma adiantoides, all of which possess annular steles and medullary strands. He adds that in the Cyatheaceous genera the medullary bundles may branch off from the annular stele, or, as in *Pteris*, the axial strand may end free in the pith in the form of a fine prosenchymatous termination.* These facts are of interest in connection with the behaviour of the axial strand of *Matonia*, which has been noticed in the foregoing description. Another point of comparison is afforded by METTENIUS' description of the petiolar stele in *Dennstædia* being supplied by the outer tube and by the medullary strand in the centre of the stem. This is analogous to the contribution made by the smaller stele of *Matonia* to the vascular system of the frond, which is mainly, but not entirely, derived from the large outer stele. Finally, METTENIUS refers to the existence of an annular stele in most species of *Dennstædia* (a section of the genus *Dicksonia*), *Microlepia* (a section of *Davallia*), *Hypolepis*, and species of *Phegopteris* (a section of *Polypodium*), also in *Pteris incisa*, THUNB. (= *P. Vespertilionis* and *P. aurita*), and *Polypodium Wallichii*, R. BR.†

We find subsequent references to annular gamosteles in DE BARY'S 'Comparative Anatomy,‡ where several genera are quoted as having a tubular vascular system with a relatively small foliar gap at each node.

VAN TIEGHEM and DOULIOT§ compare the closed ring of *Dennstædia* and other ferns with the gamostelic structure of *Auricula japonica.*

We see, then, that the annular form of stele usually associated with *Marsilia* and *Pilularia*, and described by LECLERC DU SABLON|| in embryonic stems of *Pteris* and other genera, is found also in the adult rhizomes of several ferns, notably in members of the Cyatheaceæ and Polypodiaceæ; it occurs, too, in the genus *Loxsoma.* The occurrence of one or more axial strands of xylem enclosed by phloem in *Dicksonia* (*Dennstædia*) *rubiginosa* and other ferns affords a close parallel with the *Matonia* type of structure.

In *Dicksonia rubiginosa* the outer stele differs from that of *Matonia* in having the protoxylem groups in small bays, or rather in loops of the xylem band, towards the outer surface, and not on the inner edge as in *Matonia.* Similarly, in *Dicksonia davallioides*, R. BR., the protoxylem is slightly internal in the xylem band and near the outer surface. In *Davallia Speluncæ*, BAKER, *D. strigosa*, SWARTZ, *Pteris incisa*, THUNB., and *Hypolepis tenuifolia*, BERNH., the breadth of the annular stele is much less regular than in *Matonia pectinata.* In *Loxsoma*, on the other hand, the protoxylem groups are said to be indistinguishable.¶ In the genus *Platyzoma*,

---

* METTENIUS (64), p. 502.

† *Ibid.*, p. 543, Plate 7 (figures of *Dennstædia*, &c.). The nomenclature adopted is that of the *Synopsis Filicum* [HOOKER and BAKER (68)].

‡ DE BARY (84), p. 284. *Vide* also TANSLEY (96), p. 140, DANGEARD (89), and SADEBECK (79), p. 282.

§ VAN TIEGHEM and DOULIOT (86), p. 313.

|| LECLERC DU SABLON (90).

¶ For this fact I am indebted to Mr. GWYNNE-VAUGHAN.

referred to by BROWN as possessing a closed vascular ring, there is no phloem on the inner side of the xylem. On the whole, perhaps, *Dicksonia rubiginosa* approaches most closely to the structure of *Matonia*, but our knowledge of the anatomy of gamostelic ferns is far from satisfactory, and we do not possess the necessary data for a detailed comparison of *Matonia pectinata*, as regards the anatomy of the stem and the mode of origin of the leaf steles, with other genera having a somewhat similar structure. Work now in progress by Messrs. GWYNNE-VAUGHAN, BOODLE, and others should yield results of special value from the point of view of fern anatomy and as regards the systematic value of particular structural features. It is, however, safe to conclude that the annular form of stele is not of great systematic importance, but so far as our comparison has gone it would seem that the Cyatheaceæ present a closer agreement than other families with *Matonia*, as regards the stelar anatomy. In addition to the difference in the position of the protoxylem groups, there are other points, such as the larger size of the sieve-tubes and the greater breadth of the phloem, in which *Dicksonia rubiginosa* differs from *Matonia*. There is a striking resemblance, as Mr. A. G. TANSLEY reminds me, between the third (axial) stele of *Matonia* and the "cord of metaxylem derived from the inner margin of the cylindrical stele" of *Selaginella lævigata*, BAKER, var. *Lyallii*, SPR.*

The occurrence of multicellular hairs on the rhizome instead of the more usual paleæ is a feature worthy of notice. RUSSOW† describes hairs as common in the Cyatheaceæ and Hymenophyllaceæ, and as occurring also in members of the Osmundaceæ and Schizaceæ, but rare among Polypodiaceous ferns. GOEBLER‡ mentions the multicellular hairs of *Lygodium japonicum*, Sw.; and PRANTL§ speaks of them in species of *Lygodium, Schizæa*, and *Anemia*. POIRAULT|| quotes examples of some Polypodiaceæ in which the rhizome bears long hairs.

As regards the sieve-tubes of *Matonia*, we find a similar form in Cyatheaceous genera¶; also in *Osmunda*** and other ferns.

The occurrence of hairs and the structure of the sieve-tubes, with numerous lateral plates, are not at variance with the comparison already made with the Cyatheaceæ.

β. Leaf.

The presence of a single petiolar stele is a feature of no great value from a comparative point of view; it is met with in representatives of the Osmundaceæ,

---

* GIBSON (94), p. 194.

† RUSSOW (72), p. 85.

‡ GOEBLER (86), p. 453, Plate 11, fig. 20.

§ PRANTL (81), p. 37.

|| POIRAULT (94), p. 162.

¶ THOMAE (86), Plate 8, fig. 8.

** ZENETTI (95), Plate 2, fig. 5, and JANCZEWSKI (82), Plate 3, fig. 6.

Hymenophyllaceæ, Schizaceæ, Gleicheniaceæ, and Polypodiaceæ.* Presl† long ago expressed the view that the form of the leaf " bundle " is rarely useful in distinguishing genera, but in Gleicheniaceæ and Cyatheaceæ the shape of the single vascular band is fairly characteristic. The *Matonia* petiolar stele resembles that of several species of Cyatheaceous ferns. The occurrence of parenchyma among the xylem tracheids is another character shared by *Matonia* and the Cyatheaceæ ; but this tissue is found also in the steles of many other ferns. The existence of fibrous cells in the stele has been noticed in *Trichomanes*, *Anemia*, *Gleichenia*, and in species of *Schizæa*.‡

In the description of the petiolar stele of *Matonia*, reference was made to the conspicuous strands of loose thin cells accompanying the protoxylem groups. Similar strands are especially well marked in the vascular tissue of Cyatheaceus ferns ;§ but they occur also in *Osmunda*|| and other genera.

γ. *Root.*

The triarch structure of the roots suggests a comparison with some Cyatheaceæ¶, but the same form of root cylinder occurs in species of *Botrychium*, *Ophioglossum Helminthostachys*, and *Todea*, and in species of Gleicheniaceæ and Hymenophyllaceæ.**

Enough has been said to show that *Matonia* has many points of contact with various fern families, but the sum of resemblances is the greatest between this genus and the Cyatheaceæ. Several writers have drawn comparisons between the sori of *Matonia* and those of the Cyatheaceæ, but neither in this respect nor in the anatomical structure is there sufficient similarity to render advisable the inclusion of the Malayan genus among the Cyatheaceæ.

The facts of anatomical structure lend support to the retention of the Matonineæ as a distinct sub-division of the Filices, represented by a single genus and two species,—isolated surviving ferns of a long line of extinct species, which flourished in the Jurassic and Cretaceous epochs. We may next briefly consider some of the fossil representatives of the Matonineæ, paying special attention to their geological and geographical range.

D. Fossil Matonineæ.

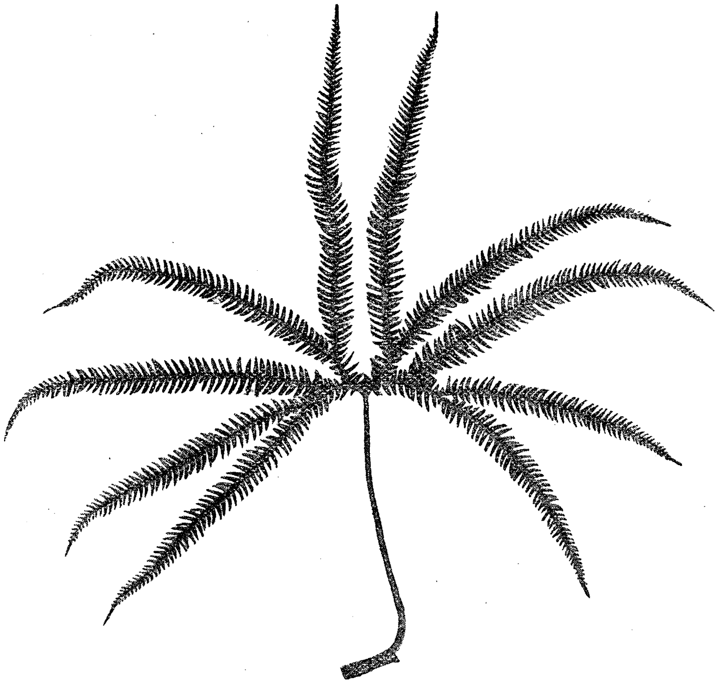
The statement that the Matonineæ were well represented during the Mesozoic epoch rests on evidence derived in part from the nature of the sori and sporangia, and in part from the characteristic habit of certain fossil fronds.

---

* Thomae (86), p. 14.
† Presl (47), p. 2.
‡ De Bary (84), p. 447.
§ Thomae (86), p. 126.
|| Terletzki (84), p. 494.
¶ v. Tieghem (70), p. 70.
** Poirault (94), p. 135. *Vide* also De Bary (84), p. 363.

As a rule comparisons based on venation characters and on the form of the frond are of secondary importance, and in some cases practically valueless. In *Matonia pectinata*, however, we have a frond of exceptional form, at least among living ferns. Some species of *Gleichenia* bear leaves having an apparently similar habit, but on careful comparison the fronds of this genus may be distinguished by the characteristic forking of their pinnæ. The New Zealand species represented in fig. 7, *Gleichenia Cunninghami*, HEW.,* bears a superficial resemblance to that of *Matonia pectinata*, but the branching of the pinnæ is sufficiently obvious to render it distinct from the latter species, in which the leaf-stalk appears to bend over at the summit in the form of two scorpioid cymes.† The anastomosing veins below the *Matonia* sorus and the more falcate pinnules are other features—apart from the structure of the sori—which furnish additional differences.‡

Fig. 7.



Gleichenia Cunninghami, HEW., from a specimen in the Cambridge Herbarium.
(Photograph by Mr. EDWIN WILSON.)

Under the various species to which reference is made in the following list, no

---

* From a specimen in the Cambridge Herbarium, gathered on the Cheviot Hills, Middle Island, N.Z., at a height of 1000 feet.

† ZEILLER (85), p. 21.

‡ [Since the above was written my attention has been drawn by Mr. BAKER to a new species of *Polypodium*, *P. palmatopedatum*, BAKER (Kew Herbarium, No. 353*), recently obtained by Dr. HENRY from Yunnan, China. The habit of the frond is very similar to that of *Matonia pectinata*, but the lamina is divided into lanceolate segments bearing large oval sporangia on each side of the main veins (BAKER; Kew Bulletin, 1898, p. 232.]

attempt has been made to append a complete synonymy; but to prevent confusion a few synonyms are given in the case of species which have been described under different names, and have not hitherto been considered identical. The evidence on which I have ventured to reduce the number of specific names has been furnished by a comparative examination of various type-specimens in the British and other Museums.

To discuss in detail the systematic position of all known fossil fronds which might reasonably be included in an enumeration of possible representatives of Matonineæ, would involve a lengthy and tedious examination of numerous diagnoses published during the last seventy years.

SOLMS-LAUBACH* in his text-book speaks of the genera *Laccopteris*, *Selenocarpus*, *Andriania*, *Clathropteris*, *Dictyophyllum* as leptosporangiate ferns, which agree in certain characters with both the Gleicheniaceæ and Cyatheaceæ. *Microdictyon*, *Gutbiera*, and *Carolopteris* may be added to this list as closely allied genera. SCHUMANN† and other writers express similar views as to the systematic position of some or all of these Mesozoic genera.

In a Fossil Flora of Jurassic rocks from the neighbourhood of Cracow, RACIBORSKI‡ includes the genera *Laccopteris* and *Microdictyon* in the family Matonineæ.

The genera *Selenocarpus*,§ *Clathropteris*, and *Dictyophyllum* need not be discussed, as they do not present so close a resemblance to *Matonia* as do other types, such as *Laccopteris* and *Matonidium*. The genus *Andriania*,‖ instituted in 1843, by BRAUN, for a Rhætic fern from Bayreuth, bears a striking resemblance to *Matonia pectinata* as regards the form of the frond, but the sori and veins differ from those of the recent species.

Laccopteris.

This genus was instituted by PRESL in 1838¶ for some fragments of fern fronds from the Keuper of Strullendorf; the circular sori—which are represented in PRESL's figure as consisting of five sporangia—and the veins are compared with those of *Gleichenia*. The type-species is *L. elegans*, and the generic characters are given by PRESL as follows:—

"Frons pinnata, nervi primarii excurrentes, nervi secundarii dichotomi ramulis furcatis simplicibusve, mediis in medio dorso soriferis. Sori biseriales, foveæ semiglobosæ immersi, e sporangis compositi."

In 1841 GÖPPERT** described several well-preserved impressions of ferns from the

---

* SOLMS-LAUBACH (91), p. 154.

† SCHUMANN (94), p. 174.

‡ RACIBORSKI (94), p. 39.

§ SCHENK (67), p. 89, Plate 22.

‖ BRAUN (43), Plate 10. *Vide* also SCHENK (67), p. 87, Plates 21 and 22; ANDRAE (53), Plate 7, figs. 1–3.

¶ In STERNBERG (38), p. 115, Plate 32, fig. 8.

** GÖPPERT (41), Lief. 1 and 2, Pls. 5 and 6.

Lias of Bayreuth, which he referred to PRESL'S genus *Laccopteris*, and compared them with recent Gleicheniaceæ. GÖPPERT'S figures illustrate very clearly the habit of the frond, and the position of the annulus of the sporangia is fairly well shown. A more detailed description of the genus is given by SCHENK* in his 'Fossil Flora' of 1867, in which PRESL'S species, *L. elegans*, is re-described, and two new Rhætic species instituted, *L. Göpperti*, and *L. Münsteri*. The lateral veins of the pinnules are represented as dichotomosing and not anostomosing, and the character of the sorus and sporangia is fully described. SCHIMPER† subsequently includes *L. Göpperti* as a synonym of PRESL'S species, *L. elegans*. SCHENK compares the fructification with that of the Gleicheniaceæ, but the habit of the frond he recognises as practically identical with that of *Matonia pectinata*. The very close affinity between the Mesozoic fern *Laccopteris* and the recent *Matonia*, was, however, first demonstrated by ZEILLER;‡ he showed that not only in the form of the frond, but in the size, disposition, and structure of the sporangia and spores, the two genera are practically identical. The circular sori of *Laccopteris* seem to have been without an indusium, and another difference is noticed in the absence of any anastomosing of the veins in the basal portions of the pinnules in the fossil fronds, such as occurs below the sori in *Matonia*. The frond represented in text, fig. 8, from the Keuper of Bayreuth is no doubt *Laccopteris Göpperti*, SCHENK§ (= *L. elegans*, PRESL); the venation is unfortunately very imperfectly present, but in a few pinnules enough can be seen to show undoubted lateral anastomosing of the veins, as shown in the slightly enlarged drawing of a portion of an ultimate segment. The presence of anastomoses of the veins connects still more closely *Laccopteris* and *Matonia*. This type of venation, not previously associated with *Laccopteris*, is identical with that of BRONGNIART'S genus, *Phlebopteris*,‖ and but slightly different from that of SAPORTA'S genus *Microdictyon*,¶ and *Carolopteris*** of DEBEY and ETTINGSHAUSEN. Without examining the type-specimens of GÖPPERT or SCHENK it would be rash to assume that the venation characters of *Laccopteris* have been incorrectly described; but the occurrence of anastomosing veins in a frond, which is undoubtedly identical with one of SCHENK'S species, leads one to incline to the view that there is no essential difference between the fossil ferns—mostly of Rhætic age—referred to *Laccopteris* and the Jurassic species placed by some writers in the genus *Phlebopteris*.††

---

* SCHENK (67), p. 93, Pls. 22–25. There are some good specimens of these species in the GÖPPERT collection of fossil plants in the Breslau Museum.

† SCHIMPER (69), p. 580.

‡ ZEILLER (85).

§ *Cf.* SCHENK (67), Plate 23.

‖ BRONGNIART (28), p. 372, and (49), p. 30.

¶ SAPORTA (73), p. 305, Plate 33, figs. 2–7.

** DEBEY and ETTINGSHAUSEN (59), p. 26, Plate 3.

†† [Since writing the above I have examined additional specimens of *Laccopteris* in the Berlin Geological Museum, and found the veins distinctly anastomosed.]

To discuss in detail the question of generic identity of certain Mesozoic ferns would take us beyond the primary aim of this paper, which is to mention such fossil species as may reasonably be included in the Matonineæ. In view of the identity in the form of the fronds and the close agreement as regards the sori, sporangia, spores and anastomosing veins in *L. elegans*, I propose to include the species hitherto referred to *Laccopteris*, and those assigned by several authors to *Phlebopteris*, under the former generic name. In this more comprehensive sense the genus *Laccopteris* may be defined as follows:

Fig. 8.

Laccopteris elegans (Presl). From a specimen (No. 500) in the British Museum, Lower Keuper, Bayreuth. Frond nat. size; pinnule × 3. (Drawn by Miss G. M. Woodward.)

Fronds pedate, in habit like those of *Matonia pectinata*, R. Br., with pinnate or pinnatifid pinnæ; ultimate segments linear in form, with a well-marked midrib giving off numerous secondary veins which branch dichotomously, and are in places connected by short lateral anastomoses. Sori* circular, forming a single row on each side of the midrib; the sporangia usually few in number, from 5 to 14, with an oblique annulus and tetrahedral spores.

---

* The sori of *Laccopteris* have been hitherto described as non-indusiate, but it is difficult to be certain as to the absence of an indusium.

The venation of *Matonia pectinata* is especially interesting in the comparison of fossil fronds; the occasional lateral anastomoses, and the close approach to the *Woodwardia* type of venation shown in Plate 18, fig. 23, agree exactly with the *Phlebopteris* character, while the forked and separate lateral veins are identical with those usually associated with the fossil fronds referred to *Laccopteris* (*cf.* text-fig. 9, A–C).

Before enumerating fossil species of *Laccopteris*, a brief reference must be made to the genus *Phlebopteris*, which it is now proposed to include under the former designation.

BRONGNIART instituted the generic name *Phlebopteris* in 1828,* and modified the diagnosis in 1849.† The anastomosing of the lateral veins in "arcades" close to the midrib (fig. 9, B), and the origin of simple or forked veins from the arched anastomoses are characters on which especial stress is laid; the venation is in fact precisely that of *Matonia pectinata*. The occurrence of lateral anastomoses and arcade-like connections in *Matonia*, combined with secondary forked veins not laterally connected, serves to emphasise the probability that the supposed difference in the venation characters of *Laccopteris* and *Phlebopteris* is of little or no value.‡

The following list must not be regarded as including all known species of *Laccopteris* or *Phlebopteris;* only some of the more satisfactory examples are mentioned,§ and in a few cases synonyms are given to illustrate the probable identity of leaves frequently referred to distinct species:—

Laccopteris elegans, PRESL. From the Rhætic beds of Germany. Text-fig. 8 illustrates the habit of this type of frond. For additional drawings, reference must be made to GÖPPERT,|| SCHENK,¶ and other authors. This species is recorded also from Bornholm by BARTHOLIN.**

L. Münsteri, SCHENK. Rhætic of Germany. This species closely resembles *L. elegans.* The sori, sporangia, and spores have been described and figured by SCHENK,†† ZEILLER,‡‡ and others. There is a very close resemblance between this fern as figured by SCHENK, and specimens of *L.* (*Phlebopteris*) *polypodioides*, BRONGN., from the Lower Oolite rocks.

---

* BRONGNIART (28), p. 372.

† *Ibid.* (49), p. 30.

‡ Since writing this I find that NATHORST has expressed the opinion that *Phlebopteris polypodioides* presents a very close agreement with *Laccopteris* and *Andriania*, and might well be referred to one of these genera.—NATHORST (80), pp. 60–61.

§ Other species are incidentally referred to in the list of countries from which probable representatives of the Matoninæ have been recorded.

|| GÖPPERT (41).

¶ SCHENK (67).

** BARTHOLIN (94), p. 21, Plates 8 and 9.

†† SCHENK (88), fig. 30, p. 38.

‡‡ ZEILLER (85).

L. polypodioides, Brongn. Lower Oolite, Gristhorpe, near Scarborough. This species was first described by Brongniart.* In general habit it agrees with the older species of *Laccopteris;* the sori appear to consist of a somewhat large number of sori, as many as 13 or 14 being visible in some cases.† The annulus resembles that in *L. elegans* as described by Schenk and Zeiller. A portion of a segment of this species is represented in Text-fig. 9, B; two of the sori, of about 12 to 14 sporangia, are clearly preserved at *S*, *S*; the position of the other sori is indicated by the smaller veins, which are faintly indicated, with occasional anastomoses.

Laccopteris polypodioides (Brongn.), 1828.

Phlebopteris propinqua, Brongniart (28), p. 373, Plate 132, fig. 1, and Plate 133, fig. 2.
Pecopteris cæspitosa, Phillips (29), p. 148, Plate 8, fig. 10. (Type-specimen in the York Museum.)
Pecopteris crenifolia, Phillips (29), p. 148, Plate 8, fig. 11. (Type-specimen in the York Museum.)
Pecopteris polypodioides, Lindley and Hutton (31), vol. 1, Plate 60.
Phlebopteris contigua, Lindley and Hutton (33), vol. 2, Plate 144. (Type-specimen in the Scarborough Museum.)
Pecopteris propinqua,‡ Lindley and Hutton (33), Plate 119. (Type-specimen in the Scarborough Museum.)
Hemitelites Brownii, Göppert (36), p. 334, Plate 38, fig. 1.
Polypodites crenifolius, *ibid.*, p. 343.
Hemitelites polypodioides, *ibid.*, p. 336, Plate 15, figs. 8 and 9.
Polypodites Lindleyi, *ibid.*, p. 342, Plate 38, figs. 5 and 6.
Steffensia polypodioides, Presl in Sternberg (38), p. 125.
Steffensia crenifolia, *ibid.*, p. 124.
Polypodites Lindleyi, Zigno (56), p. 162.
Phlebopteris crenifolia, Phillips (75), p. 202.
Phlebopteris Lindleyi, *ibid.*, p. 202.
Phlebopteris contingua, *ibid.*, p. 202.
Pecopteris cæspitosa, *ibid.*, p. 207, Plate 8, fig. 10 (*non* Lign. 20).

Some fragments described by Brongniart from a Jurassic horizon in Bornholm as *Phlebopteris Schouwii*§ may possibly be identical with *P. polypodioides.*

---

* Brongniart (28), p. 372, Plate 83, fig. 1.

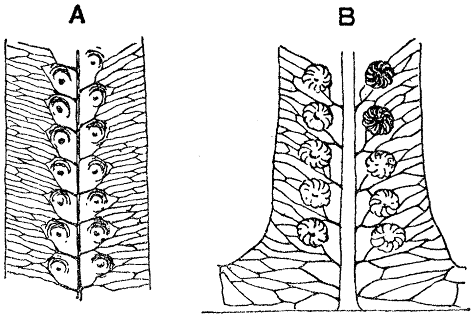
† Specimen No. 52522, in the British Museum, shows the sori very clearly. This and other Jurassic plants will be figured and described in a forthcoming British Museum Catalogue of Jurassic plants.

‡ Nathorst (80), p. 60, has also pointed out the identity of *P. propinqua*, *P. polypodioides*, and *P. crenifolia.*

§ Brongniart (28), p. 374, Plate 132, figs. 4–6.

The specimen described by LECKENBY* in 1864 as *Phlebopteris Woodwardi* (type-specimen in the Woodwardian Museum, Cambridge), is very similar to, if not identical with, *L. polypodioides.* LECKENBY'S type-specimen consists of an imperfect pinnule, showing the impressions of circular sori and lateral veins with numerous anastomoses; it is certainly identical with the fragment (6 millims. broad) from the Inferior Oolite of Yorkshire, represented in fig. 9, A. It is also, in all probability, specifically identical with SAPORTA'S *Microdictyon Woodwardianum,*† and this differs very slightly from another French species founded by the same author on some small pinnule fragments from the Jurassic (Bathonian and Oxfordian) rocks of France.‡ The portion of a pinnule shown in fig. 9, C, from the Inferior Oolite of Stamford is also most probably specificially identical with *Laccopteris polypodioides;* it shows the anastomosing veins below the sori, as in *Matonia;* the sporangia themselves have not been preserved.

Fig. 9.



A.—Pinnule of *Laccopteris Woodwardi* from the Inferior Oolite of Yorkshire, showing reticulate veins and hemispherical bosses with a small central depression, marking the position of circular sori which were attached to a central receptacle (No. 217, British Museum).

B.—Pinnule of *Laccopteris polypodioides,* with sori and soral impressions, Upper Shale, Gristhorpe Bay (No. 2522, British Museum).

C.—Pinnule fragment from the Inferior Oolite of Stamford (No. 52867, British Museum).

(From drawings by Miss G. M. WOODWARD.)

This brings us to the question of the possible identity of the genus *Phlebopteris* of BRONGNIART (*Laccopteris*) and *Microdictyon* of SAPORTA. SAPORTA instituted the latter genus for some detached pinnules of Jurassic ferns, which he considered did not conform in all points to either *Phlebopteris* or *Thaumatopteris;* from the former genus *Microdictyon* is said to differ in the presence of a reticulum of veins in the large meshes formed by the anastomosing of the secondary veins, and from the latter in the disposition of the sori. We are not concerned with *Thaumatopteris,* as the characteristics of this genus separate it in certain respects from the *Matonia* type.

---

* LECKENBY (64), p. 81, Plate 8, fig. 6.

† SAPORTA (73), p. 313, Plate 33.

‡ *Ibid.,* p. 309, Plates 33, 35, and 44.

Several Jurassic and Cretaceous ferns have been placed in SAPORTA's genus by various authors, and I have elsewhere* retained *Microdictyon* as a distinct generic type. In habit *Microdictyon* agrees with *Phlebopteris*† and *Matonia pectinata*, but the sori appear to be smaller than in *Phlebopteris*, and the smooth rounded outline of the closely set rows of the hemispherical soral projections suggests the presence of a circular indusium attached to a central receptacle; or the projections with a central hole may be casts of the cup-like depressions left on the fall of the sori, as shown in the *Matonia* pinnule of fig. 14, Plate 18. SAPORTA and other authors do not refer to the presence of an indusium; and RACIBORSKI‡ describes some Polish species as being without an indusium, but his figures favour the idea that an indusium may have been present. The fragments from the Aachen chalk, figured by DEBEY and ETTINGSHAUSEN§ as species of *Carolopteris*, and no doubt identical with *Microdictyon*, are described as indusiate. It may be that in *Laccopteris* there was no indusium, but in *Microdicyton* the sori were indusiate. ZEILLER,‖ in a footnote to his paper on Tong-King fossils, refers to a figure by HEER of *Laccopteris* as suggesting the presence of an indusium, but in his later paper¶ he considers the sori to have been naked. It is exceedingly difficult to determine whether or no an indusium was present in these fossil sori, and the ease with which the indusium of *Matonia* is detached emphasises the danger of drawing conclusions as to the indusiate or non-indusiate condition of certain kinds of fossil sori. The fossil *Matonidium* was probably indusiate, and the appearance of some at least of the species referred to *Microdictyon* points undoubtedly to the existence of an indusium; the occurrence of fertile pinnæ of *Laccopteris* in which the outline of the sporangia are distinctly shown, is no proof that an indusium was never present. In an older leaf, which had been exposed to the air before being embedded in sediment, the circular indusium might very readily fall off. The fact, therefore, that in some of the specimens referred to *Microdictyon* the sori appear to be indusiate, does not in itself afford an obstacle in the way of uniting SAPORTA's *Microdictyon* to *Laccopteris* (including *Phlebopteris*).

Specimens conforming to the *Laccopteris* (*Microdictyon*) type have been recorded from Jurassic and Cretaceous rocks of England,** Germany, France, Portugal, Belgium, Austria, Italy, Russia, Bornholm, Switzerland, Australia, and elsewhere.

It is probable that the fragments of a fern described by HEER†† from the Cretaceous

---

* SEWARD (94), p. 134.

† SCHIMPER in ZITTEL (90), p. 136, also suggests that *Microdictyon* is scarcely separable from *Phlebopteris*.

‡ RACIBORSKI (94), p. 42, Plate 13, fig. 10.

§ DEBEY and ETTINGSHAUSEN (59), Plate 3, figs. 20–27.

‖ ZEILLER (82), p. 347.

¶ ZEILLER (85), p. 22.

** *Vide* SEWARD (94), p. 134; VELENOVSKY (88); BARTHOLIN (92), Plate 10; HEER (76), Plate 4, &c.

†† HEER (80), p. 7, Plate 1, figs. 1–6.

beds of Pattorfik, in Greenland, under the generic name *Nathorstia*, may belong to *Laccopteris;* if this be so, the northern range of the Matonineæ is considerably extended. An examination of the original specimens figured by HEER, and now in the Stockholm Palæobotanical Museum, led me to compare *Nathorstia* with *Laccopteris.* There is a close resemblance also between some pinnæ described by HEER[*] from the Upper Chalk of Greenland as *Cyathea angusta* and the *Matonia* type of frond. Another genus which should probably be included in *Laccopteris* is the monotypic *Guthiera* of PRESL,[†] described by PRESL and SCHENK,[‡] and more recently recorded from Sweden[§] and Portugal.[||]

Another instance of a Matonia-like habit is afforded by some small Italian Oolitic ferns referred to ZIGNO to the genus *Marzaria* ;[¶] this name has also been applied to a small palmate leaf from the Inferior Oolite of the Yorkshire coast,[**] but the type-specimen of PHILLIPS' species, now in the Whitby Museum, has no claim to generic autonomy; both the Yorkshire and Italian leaves are most probably young fronds of *Laccopteris*, *Dictyophyllum*, or some other genus.

Matonidium.

SCHENK proposed this generic name in 1871[††] for fossil fronds having the same characters as those of *Matonia pectinata.* ZEILLER, in discussing the affinities of *Laccopteris*, points out that *Matonidium* differs from the recent genus in the more oval form of the sori, and—in some fossil species—in the larger number of sporangia. Unfortunately, no specimens of *Matonidium* have so far been found which enable us to make out in detail the structure of the sporangia, but the form of the sorus, and so much as is known of the sporangia, afford evidence of a distinct similarity to the recent species. In habit, and in the form and venation of the pinnules, *Matonidium* is practically identical with the Malayan species. This genus is characteristic of Jurassic and Lower Cretaceous rocks. It is a difficult question to decide if the Wealden species *M. Göpperti* (ETT.) and the Jurassic species *M. polydactyla* (DUNK.) are identical; they present a very strong resemblance to one another, and following LECKENBY[‡‡] in my description of the English Wealden species[§§] I ventured to regard

---

[*] HEER (83), Plate 50.

[†] PRESL in STERNBERG (38), p. 116, Plate 32, fig. 13.

[‡] SCHENK (67), p. 64, Plate 18.

[§] NATHORST (78), Plates 3 and 4.

[||] SAPORTA (94), p. 5, Plate 1, fig. 9.

[¶] ZIGNO (56), Plate 19. SCHIMPER retains this name in his account of the ferns in ZITTEL'S 'Handbuch'; but it is better to give up the genus. [ZITTEL (90), p. 130.]

[**] PHILLIPS (75), p. 204.

[††] SCHENK (71), p. 219.

[‡‡] LECKENBY (64), p. 80.

[§§] SEWARD (94), p. 63.

the two as identical. In some specimens the Wealden form has rather shorter and straighter pinnules than those of the Lower Oolite species, but this difference does not appear to be constant.

For our present purpose it is at least simpler to include both under one name; they may fairly be considered identical from the point of view of the close relationship between the fossil and living species of the Matonineæ.

Matonidium Göpperti (Ett.).

In 1846 Dunker[*] figured some imperfect portions of a fern frond from the Wealden of Northern Germany, under the names *Pecopteris polydactyla* and *P. Conybeari;* these are, no doubt, specifically identical. The same species was afterwards described and figured by Ettingshausen[†] as *Alethopteris Göpperti* from Wealden rocks of Zöbing, in Austria. Finally, Schenk substituted the generic name of *Matonidium.*[‡]

In 1864 Leckenby described some large specimens of a frond from the Lower Oolite of the Yorkshire coast, possessing a striking resemblance to *Matonia pectinata*, as *Pecopteris polydactyla.* Leckenby's original specimens are now in the Woodwardian Museum; the figures are, on the whole, accurately drawn, but the figure of the fertile pinnule does not convey a correct idea of the crowded oval sori, which cover the lower surface of the pinnules.

In the list of synonyms of *M. Göpperti* given in my Wealden Catalogue, Phillips' species, *Pecopteris cæspitosa*,[§] of Lower Oolite age, is doubtfully included; an examination of the type-specimen in the York Museum has convinced me that Phillips' specimen is a very imperfectly preserved frond of *Laccopteris polypodioides.* Bunbury[||] expressed the opinion in 1851 that if the fructification of *Pecopteris cæspitosa* were known, it would probably be found to be identical with *Laccopteris* or *Andriania.* This view is confirmed by the comparison of Phillips' type and more perfect fertile specimens of *Laccopteris.*

Matonidium Göpperti, used in the wider sense as including both Wealden and Jurassic specimens, is characterised by the usually oval—but occasionally circular—form of the crowded sori disposed in two rows on the under surface of the pinnules. The position of the central receptacle is shown by a small depression or projecting knob, according to the state of preservation, in the centre of each sorus. It is an

---

[*] Dunker (46), p. 5. For list of synonyms *vide* Seward (94), p. 63; to this list should be added *Laccopteris polydactyla* (Saporta, 'Pal. Franç.,' 1891, vol. 4., p. 384).

[†] Ettingshausen (52), p. 16, Plate 5.

[‡] The specimens figured by Schenk ('Palæontographica,' vols. 19 and 23, 1871 and 1875), are in the Berlin Bergakademie collection of fossil plants.

[§] Phillips (29), p. 148, Plate 8, fig. 10. *Pecopteris cæspitosa* has usually been regarded as a *Matonidium*, but I have no hesitation in speaking of it as identical with *L. polypodioides.*

[||] Bunbury (51), p. 187.

interesting fact that in the Jurassic fronds of this species every pinnule appears to be fertile, even the smallest segments at the base of the pinnæ, exactly as in *Matonia pectinata*.*

M. Wiesneri, KRASSER.

This species, from Cretaceous (Cenomanian) rocks of Moravia, was founded by KRASSER† for some fern fronds with a *Matonia*-like habit. *M. Wiesneri* agrees closely with the Malayan fern in the form of pinnules and in the occurrence of anastomosing veins below the sorus; the sorus appears to be indusiate and circular. KRASSER gives figures of a pinnule of the recent species,‡ but, like other authors, he overlooks the fact that the lateral veins are often connected by arching branches. The Moravian species differs from *M. Göpperti* and agrees with *Matonia pectinata* in the small number of sori on the fertile segments.

Without entering into further discussion as to the taxonomy of Mesozoic ferns allied to *Matonia*, we may briefly summarise the distribution of probable representatives of the Matonineæ. There can be little doubt that a critical comparison of the specimens described by various authors from Triassic, Jurassic and Cretaceous localities, and referred to such genera as *Laccopteris*, *Gutbiera*, *Phlebopteris*, *Microdictyon*, *Matonidium*, and others, would yield valuable results from the point of view of the past history of the Matonineæ.

The geological range of the genera referred to extends from Rhætic to Cretaceous rocks, and, geographically, the species of these genera appear to be essentially European; they are recorded from England, France, Germany, Belgium,§ Italy,|| Austria, Portugal,¶ Bornholm,** Sweden,†† Poland,‡‡ Persia,§§ and possibly Spitzbergen|||| and Greenland.¶¶ The apparent absence of such ferns from extra-European regions must be, in part at least, ascribed to our lack of data, but the Indian fossil

---

* There are some exceedingly good examples of the Jurassic *Matonidium* in the British Museum collection, and specimens are not uncommon in the iron-stained rocks on the beach at Hayburn Wyke, a well known plant locality on the Yorkshire coast.

† KRASSER (96), p. 119, Plate 11, fig. 1; Plate 12, figs. 1 and 2; Plate 17, fig. 10.

‡ *Ibid.*, Plate 17, fig. 9.

§ The collection of Bernissart Wealden plants in the Brussels Museum includes examples of *Laccopteri* (*Microdictyon*) *Dunkeri* and what are probably fragments of *Matonidium Göpperti.*

|| ZIGNO (56), pp. 172, 197, &c.

¶ SAPORTA (94). HEER (81).

** BARTHOLIN (92).

†† NATHORST (78) p. 32.

‡‡ RACIBORSKI (94). *Vide* also SEWARD (94).

§§ KRASSER (91), p. 4.

|||| NATHORST (97), p. 31.

¶¶ HEER (80).

floras, as well as those of Africa, Australia and China, do not afford any satisfactory examples which can be definitely referred to *Laccopteris, Phlebopteris, Microdictyon* or *Matonidium.*[*]

ZEILLER[†] has recorded *Woodwardites microlobus,* SCHENK, *Polypodites Fuchsi,* ZEILL., also species of *Dictyophyllum* and *Clathropteris* from the Rhætic strata of Tong-King, but none of these specimens afford any satisfactory evidence of a close affinity with *Matonia.* As ZEILLER points out, the recent genus *Dipteris* (a section of *Polypodium*) alluded to by WALLACE as growing in company with *Matonia pectinata* on Mount Ophir, may well be compared with such fossil ferns as those referred to *Clathropteris* and certain other Mesozoic genera.

A fragment of an African fern, described by TATE[‡] as *Pecopteris Atherstonci* from Africa, has been included by SCHIMPER in the genus *Laccopteris,* but as ZEILLER[§] remarks, this determination is purely hypothetical; it probably belongs to a *Cladophlebis* leaf.

Geological evidence points unmistakably to the wide European distribution of the Matonineæ in Jurassic and Lower Cretaceous times, but it is not yet sufficiently complete to enable us to understand the series of changes which led to the present isolation of *Matonia* in the Malayan region. *Matonia* may reasonably be classed among present-day survivals in the southern hemisphere of ancient Mesozoic types, and it would seem that this generic type originated in the northern hemisphere late in the Triassic or early in the Jurassic period. The apparent absence of satisfactory fossil Matonineæ in the Tertiary floras lends support to the view that this section of the Filices reached its maximum development in the Mesozoic era, and towards the close of the Cretaceous period its geographical range had become considerably restricted. Climatal conditions, and, perhaps, more particularly the revolution in the struggle for existence consequent on the appearance of the flowering plants, drove these Mesozoic types towards the south, where the environment more nearly coincided with the conditions of life which had ceased to exist in the northern hemisphere.

BIBLIOGRAPHY.

ANDRAE, K. T. (53). Fossile Flora Siebenbürgens und des Banates. Abh. k.-k. Geol. Reichs., vol. 2, Abth. iii.

BAKER, J. G. (88). On a further Collection of Ferns from West Borneo. Journ. Linn. Soc. (Bot.), vol. 24, p. 256, 1888.

---

[*] A portion of a pinna has been described by ETHERIDGE from the Ipswich Coal-Measures of Queensland, under the name *Phlebopteris Alethopteroides,* which is probably a species of *Laccopteris* (*vide* ETHERIDGE, 'Proc. Linn. Soc.,' N. S. Wales, vol. 3, 1888, p. 1306).

[†] ZEILLER (82), pp. 308, *et seq.* *Vide* also ZEILLER (97), p. 51.

[‡] TATE (67), p. 145, Plate 5, fig. 2. (The fossil plants described by TATE are in the Museum of the Geological Society.)

[§] ZEILLER (85) p. 21.

BAKER, J. G. (91). A Summary of New Ferns which have been Discovered or Described since 1874. Annals Bot., vol. 5, p. 191, 1891.

BARTHOLIN, C. T. (94). Nogle i den bornholmske Juraformation forekommende Planteforsteninger. Bot. Tiddsskrift, vol. 18, 1894.

DE BARY, A. (84). Comparative Anatomy of Phanerogams and Ferns. Oxford, 1884.

BEDDOME, R. H. (68). The Ferns of British India, vol. 2—Madras, 1868.

BOMMER, J. E. (67). Monographie de la Classe des Fougères. Bull. Soc. Roy. Bot. Belg., vol. 5, 1866. Brussels, 1867.

BOWER, F. O. (89). The Comparative Examination of the Meristems of Ferns, as a Phylogenetic Study. Annals Bot., vol. 3, p. 305.

BRAUN, F. (43), *vide* MÜNSTER, E., Graf zu. Beiträge zur Petrefactenkunde Bayreuth. Heft vi. Bayreuth, 1843.

BRONGNIART, A. (28). Histoire des Végétaux Fossiles. Paris, 1828.

—— (49). Tableau des Genres des Végétaux Fossiles. Ext. Dict. d'Hist. Naturelle. Paris, 1849.

BROWN, R. (67). Names and Notes on Indian Plants. Miscell. Bot. Works, vol. 2, p. 531. London, 1867.

BUNBURY, C. J. F. (51). On some Fossil Plants from the Jurassic Strata of the Yorkshire Coast. Quart. Journ. Geol. Soc., vol. 7, p. 179.

BURCK, W. (84). Contributions to the Fern Flora of Borneo. Ann. Jard. Bot. Buitenzorg, vol. 4, p. 90, 1884.

CHRIST, H. (97). Die Farnkräuter der Erde. Jena, 1897.

DANGEARD, P. A. (89). Essai sur l'Anatomie des Cryptogames Vasculaires. Le Botaniste, vol. 1, 1889, Fasc. vi., p. 211.

DEBEY, M. H., and ETTINGSHAUSEN, C. VON (59). Die urweltlichen Acrobryen des Kreidegebirges von Aachen und Maestricht. Denkschr. k. Ak. Wiss., Wien, vol. 17, p. 185.

DUNKER, W. (46). Monographie der norddeutschen Wealdenbildung. Braunschweig, 1846.

ETTINGSHAUSEN, C. VON (52). Beitrag zur näheren Kenntniss der Flora der Wealden-Periode. Abh. k.-k. Geol. Reichs., vol. 1, Abth. iii., 1852.

—— (65). Die Farnkräuter der Jetztwelt. Wien, 1865.

GIBSON, R. J. H. (94). Contributions towards a Knowledge of the Anatomy of the Genus *Selaginella*, SPR. Annals Bot., vol. 8, p. 133.

GOEBLER, E. (86). Die Schutzvorrichtungen am Stammscheitel der Farne. Flora, 1886, p. 451.

GÖPPERT, H. R. (36). Die fossilen Farnkräuter. Nova Acta A. Cæs. Leop.-Car., vol. 17, Suppl. 1836.

—— (41). Die Gattungen der fossilen Pflanzen. Bonn, 1841.

HEER, O. (76). Flora fossilis Helvetiæ. Zurich, 1876.

HEER, O. (80). Nachträge zur fossilen Flora Grönlands. Kongl. Svensk. Vet.-Akad. Hand., vol. 18.

—— (81). Contributions à la Flore Fossile du Portugal. Secc. Trab. Geol. Portugal, 1881.

—— (83). Flora Fossilis Arctica, vol. 7. Zurich, 1883.

HOFMEISTER, W. (63). On the Germination, Development, and Fructification of the Higher Cryptogamia. London, 1863.

HÖHNEL, F. VON (77). Über den Kork und verkorkte Gewebe überhaupt. Sitz. k. Akad. Wiss., Wien, vol. 76, Abth. i., p. 507, 1877.

HOOKER, W. J. H., and BAUER (42). Genera Filicum. London, 1842.

—— (64). Species Filicum, vol. 5. London, 1864.

—— and BAKER, J. G. (68). Synopsis Filicum. London, 1868.

HORSFIELD, J.; BROWN, R., and BENNETT, J. J. (38). Plantæ Javanicæ rariores. London, 1838–52.

JANCZEWSKI, E. DE (82). Études comparées sur les Tubes Cribreux. Ann. Sci. Nat. [6], vol. 14, p. 50, 1882.

KLEIN, L. (84). Vergleichende Untersuchungen über Organbildung und Wachsthum am Vegetationspunkt dorsiventraler Farne. Bot. Zeit., 1884, p. 577.

KRASSER, F. (91). Über die fossile Flora der Rhätischen Schichten Persiens. Sitz. k. Akad. Wiss., Wien, vol. 100, Abth. i.

—— (96). Die fossile Kreideflora von Kunstadt in Mähren. Beit. Paläont. und Geol. Österreich-Ungarns, *etc.* Wien und Leipzig, 1896.

LECKENBY, J. (64). On the Sandstones and Shales of the Oolites of Scarborough. Quart. Journ. Geol. Soc., vol. 20, p. 74, 1864.

LECLERC DU SABLON (90). Recherches sur la Formation de la Tige des Fougères. Ann. Sci. Nat. [7] vol. 11, p. 1.

LINDLEY, J., and HUTTON, W. (31). The Fossil Flora of Great Britain, vol. 1. London, 1831–33.

—— (33). Ditto, vol. 2, 1833–35.

LUERSSEN, C. (73). Über centrifugales locales Dickenwachsthum innerer Parenchymzellen der Marattiaceen. Bot. Zeit., 1873, p. 641.

—— (89). Die Farnpflanzen. RABENHORST's Krypt. Flora, vol. 3. Leipzig, 1889.

METTENIUS, G. (64). Über den Bau von *Angiopteris.* Abhand. k. Sächs. Ges. Wiss., vol. 6, p. 501.

—— (65). Über die Hymenophyllaceæ. *Ibid.*, vol. 7, p. 403.

MOHL, H. VON (45). Über den Bau des Stammes der Baumfarne. Vermischt. Schrift., p. 108. Tübingen.

MOORE, T. (57). Index Filicum. London, 1875.

NATHORST, A. G. (78). Om Floran i Skånes Kolförande Bildningar.—I. Floran vid Bjuf. Sveriges Geol. Unders. Stockholm, 1878.

—— (78′). Beiträge zur fossilen Flora Schwedens. Stuttgart, 1878.

—— (80). Berättelse, afgifven till Kongl. Vetenskaps-Akademien, om en med understöd af allmänna medel utförd Vetenskaplig Resa till England. Öfversigt af K. Veten.-Akad. Förhand. Stockholm, 1880, No. 5, p. 23.

NATHORST, A. G. (97). Zur Mesozoischen Flora Spitzbergens. Kongl. Sv. Vet. Akad. Hand., vol. 30.

PHILLIPS, J. (29). Illustrations of the Geology of Yorkshire. York, 1829.

—— (75). Ed. III. London, 1875.

POIRAULT, G. (94). Recherches Anatomiques sur les Cryptogames Vasculaires. Ann. Sci. Nat. [8], vol. 18, 1894.

PRANTL, K. (81). Untersuchungen zur Morphologie der Gefässkryptogamen. Heft ii.—Schizaceæ. Leipzig, 1881.

PRESL, K. B. (47). Die Gefässbündel im Stiele der Farn. Abh. k. Böhm. Ges. Wiss. [5], vol. 5, 1847.

RACIBORSKI, M. (94). Flora Kopalna Krakow. Pamietn. Wydz. Akad. Umiej Krakowie, vol. 18, p. 142, 1894.

RUSSOW, E. (72). Vergleichende Untersuchungen. Mém. Acad. Imp. St. Pétersbourg [7], vol. 19.

SADEBECK, R. (79). Die Gefässkryptogamen. SCHENK'S Handbuch der Botanik, vol. 1. Breslau, 1879.

SAPORTA, G. DE (73). Plantes Jurassiques. Pal. Franç. [2], vol. 1.

—— (94). Flore Fossile du Portugal. Trav. Géol. Portugal, 1894.

SCHENK, A. (67). Die fossile Flora der Grenzschichten der Keupers und Lias Frankens. Wiesbaden, 1867.

—— (71). Die Flora der Norddeutschen Wealdenformation. Palæontograph. vol. 19, p. 203.

—— (88). Die fossilen Pflanzenreste. Breslau, 1888.

SCHIMPER, W. P. (69). Traité de Paléontologie Végétale, vol. 1, 1869.

SCHUMANN, K. (94). Lehrbuch der systematischen Botanik. Stuttgart, 1894.

SCOTT, D. H. (94). Recent Work on the Morphology of Tissues in the Higher Plants. Science Progress, vol. 1, p. 463.

SEWARD, A. C. (94). The Wealden Flora, vol. 1. Catalogue Mesozoic Plants, Brit. Mus. London, 1894.

—— (98). A Rare Fern, *Matonia pectinata*, R. BR. British Association Report, 1898, p. 1050.

SMITH, W. (75). Historia Filicum. London, 1875.

SOLMS-LAUBACH, Graf zu (91). Fossil Botany. Oxford, 1891.

STERNBERG, C., Graf von (38). Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt. Leipzig, 1820–38. Fasc. vii., 1838.

STRASBURGER, E. (91). Über den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen. Hist. Beit., Heft iii. Jena, 1891.

TANSLEY, A. G. (96). The Stelar Theory. Science Progress, vol. 5, p. 133, 1896.

TATE, R. (67). On Some Secondary Fossils from South Africa. Quart. Journ. Geol. Soc., vol. 23, p. 139.

TERLETZKI, P. (84). Anatomie der Vegetationsorgane von *Struthiopteris germanica*, WILLD., und *Pteris aquilina*, L. Pringsh. Jahrb., vol. 15, p. 452, 1884.
THOMAE, K. (86). Die Blattstiele der Farne. *Ibid.*, vol. 17, p. 99, 1886.
VAN TIEGHEM, P. (91). Traité de Botanique. Paris, 1891.
—— and DOULIOT, H. (86). Sur la Polystélie. Ann. Sci. Nat. [7], vol. 3, p. 275.
VELENOVSKY, J. (88). Die Farne der böhmischen Kreideformation. Abh. k. Böhm. Ges. Wiss. [7], vol. 2, 1888.
WALLACE, A. R. (86). The Malay Archipelago. London, 1886.
WALLICH, N. (30). Plantæ Asiaticæ rariores, vol. 1. London, 1830.
ZEILLER, R. (82). Examen de la Flore Fossile des Couches de Charbon du Tong-King. Ann. Mines [8], vol. 2, p. 299.
—— (97). Revue des Travaux de Paléontologie. Rev. Gén. Bot., vol. 9.
—— (85). Sur les Affinités du Genre *Laccopteris*. Bull. Soc. Bot. France, vol. 32, p. 22.
ZENETTI, P. (95). Das Leitungssystem im Stamm von *Osmunda regalis*, L., und dessen Uebergang in den Blattstiel. Bot. Zeit., 1895, p. 53.
ZIGNO, A. DE (56). Flora fossilis Formationis Oolithicæ, vol. 1. Padova, 1856.
ZITTEL, K. A. VON (90). Handbuch der Palæontologie. Abth. ii.—Palæophytologie (SCHIMPER und SCHENK). München und Leipzig, 1890.

EXPLANATION OF PLATES.

(The microphotographs were taken by Mr. W. TAMS, Cambridge.)

PLATE 17.

Matonia pectinata, R. BR.

Fig. 1. Piece of rhizome showing the apex and young fronds, *a–e* (nat. size).
Fig. 2. Piece of rhizome with two young fronds (nat. size).
Figs. 3–6. Stages in the development of a frond (nat. size).
Fig. 7. Frond partially expanded (nat. size).
Fig. 8. Transverse section of rhizome showing two annular steles. (× 15.)
Fig. 9. Transverse section showing three steles, and four roots in different stages of growth. *px.*, protoxylem of the second annular stele. (× 15.)
Fig. 10. The inner stele of fig. 8. *px*, protoxylem; *S*, sieve-tubes; *pt*, protophloem; *e*, endodermis. (× 60.)
Fig. 11. Transverse section of rhizome immediately in front of a leaf, showing three steles, the second annular stele open at the top. R, young root. (× 15.)
Fig. 12. Portion of fig. 11, more highly magnified. (× 40.)

PLATE 18.

Matonia pectinata, R. Br.

Fig. 13. The inner face of a young pinnule. *s*, *s′*, *s′*, sori. (× 16.)

Fig. 14. A single mature pinnule, with five circular depressions, from which sori have become detached (slightly enlarged).

Fig. 15. A, diagrammatic transverse section of a young pinnule; B, portion of the lamina of A (*x*). *Ep*, upper epidermis. (× 16.)

Fig. 16. Diagrammatic transverse section of an older pinnule, with two sori.

Fig. 17. A young sorus in vertical section, showing two immature sporangia, the large central receptacle and the circular indusium; a few short scalariform tracheids below the receptacle. (× 23.)

Fig. 18. A sporangium viewed from two opposite sides, A and B, to show the incomplete oblique annulus.

Fig. 19. Two sporangia as seen in side-view of a sorus.

Fig. 20. A sorus from which the indusium has been naturally detached.

Fig. 21. A stoma in surface-view: *a*, the surface of the papillose lower epidermal cells in focus; *b*, the two guard-cells in focus. (× 240.)

Fig. 22. Stomata in different stages of development as seen in surface-view of a young pinnule. (× 240.)

Fig. 23. Portions of two pinnules which have been bleached and stained to show the veins. S, position of a sorus; A, near the apex; B, near the base of the pinnule.

PLATE 19.

Matonia pectinata, R. Br.

Fig. 24. Transverse section of rhizome, showing the inner annular stele and the axial stele. *px*, protoxylem; *pt.*, protophloem; *s*, sieve-tubes; *e*, endodermis. (× 60.)

Fig. 25. Portion of the petiole stele (*x* in the half-section of stele). P*x*, protoxylem; *Phl*, phlœm; E, endodermis; P, pericycle; *Sl*, sclerenchyma; F, fibrous cells; S, loose parenchyma next the protoxylem. (× 165.)

Fig. 26. Transverse section of a pinnule. (× 200.)

Fig. 27. A stoma in section; numerous rodlets of a pectose substance projecting into the respiratory cavity. (× 325.)

Fig. 28. Transverse section of young rhizome, to show the deeply stained xylem parenchyma. *px*, single protoxylem group of inner annular stele. (× 40.)

Fig. 29. Vertical section of rhizome apex. (× 30.)

Fig. 30. Young leaf. A, in side-view; B, in front-view; C, transverse section through the region *a b* of B; D, transverse stele through the region *c d* of B.

Fig. 31. Transverse section of petiole. (× 15.)

Fig. 32. Multicellular hair of rhizome. *m*, thin-walled growing cells at the base.

PLATE 20.

Matonia pectinata, R. Br.

Fig. 33. Transverse section of a strand of thin-walled elements (sieve-tubes, &c.) near the termination of the axial stele. (× 240.)

Fig. 34. Transverse section of the axial stele. E, endodermis; P, pericycle; *Phl*, phloem. (× 240.)

Fig. 35. Diagrammatic transverse section of rhizome, showing the axial stele continuous with the inner annular stele.

Fig. 36. Diagrammatic transverse section close to the apex of a rhizome, passing through the point of origin of the youngest leaf.

Fig. 37. Part of the outer annular stele in transverse section, showing three protoxylem groups, *px*; S, sieve-tubes; *pt*, protophloem. (× 60.)

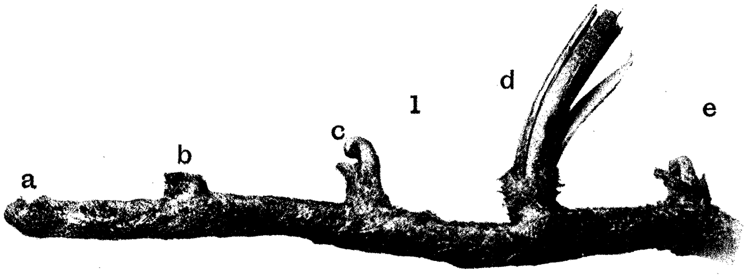
Fig. 38. Diagrammatic transverse section through the apex of rhizome. *h*, hairs bending over the apical region.

Fig. 39. Diagrammatic vertical section of rhizome apex. *P*, position of leaf-bud; R_i, R_{ii}, young roots.

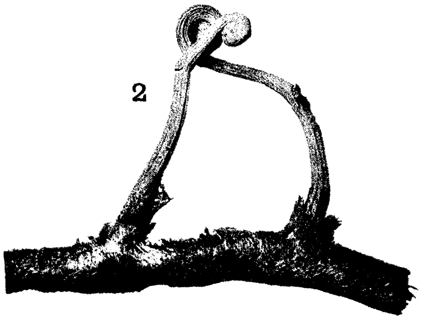
Fig. 40. Vertical section through the tip of a young pinnule. (× 325.)

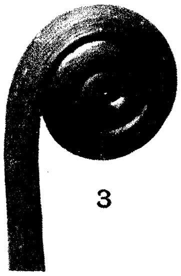
Fig. 41. Diagrammatic vertical section of a sorus, showing two sporangia and the circular indusium. A, annulus.

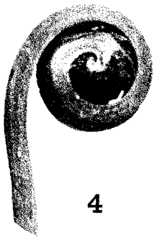
Fig. 42. Transverse section of a root. (× 70.)

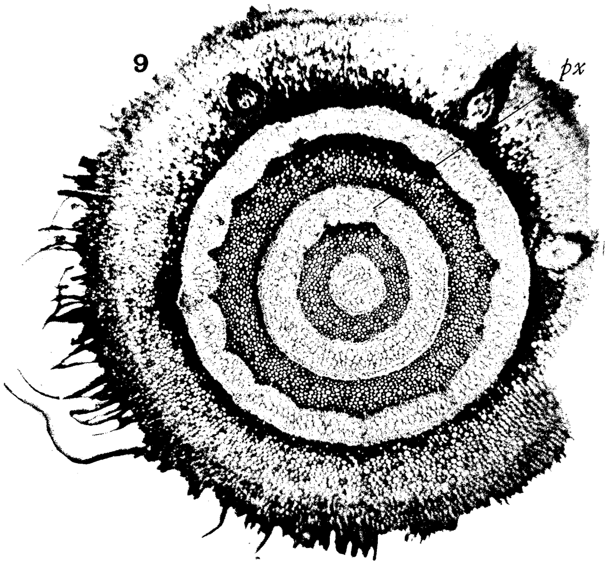

1

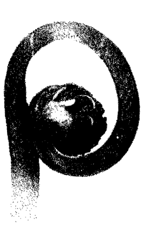

8

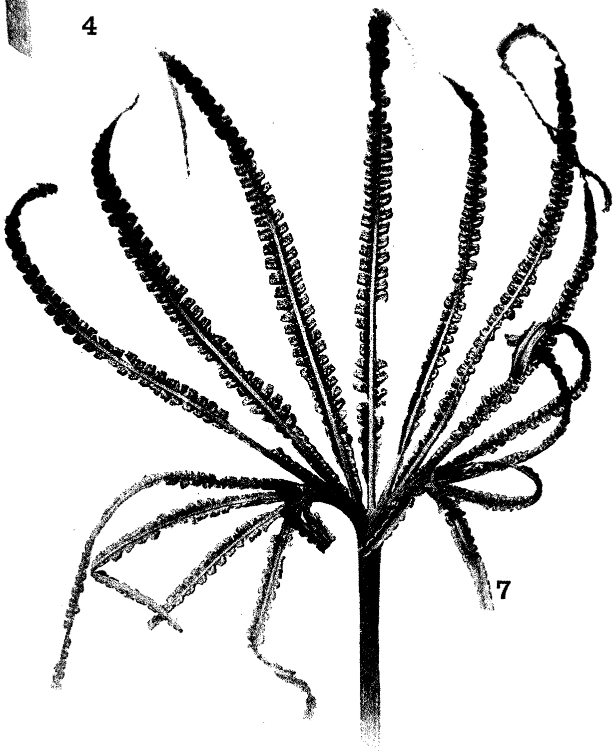

2

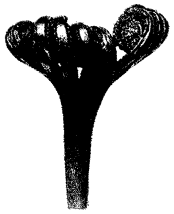

3

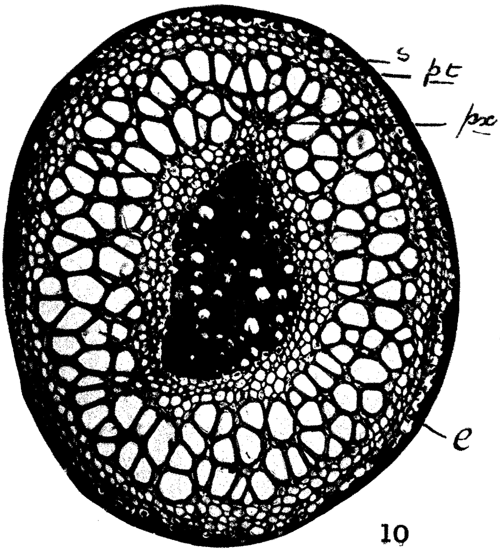

4

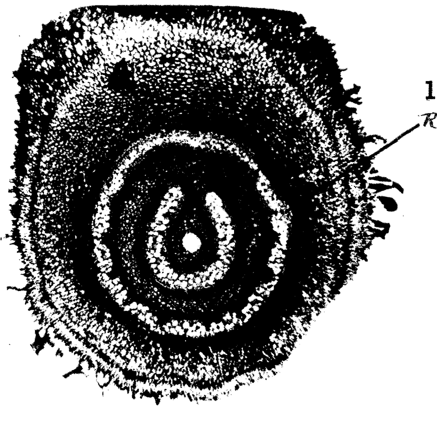

9


5

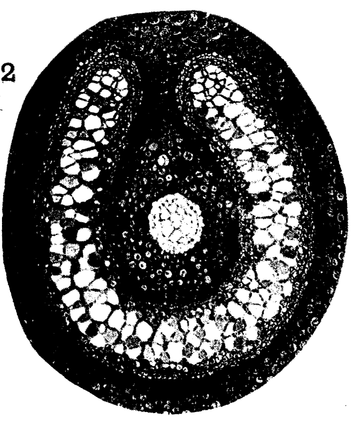

7

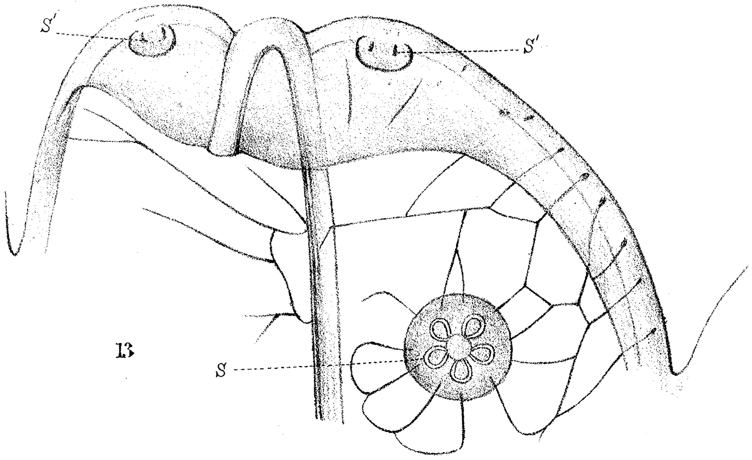

6

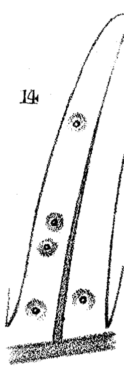

10

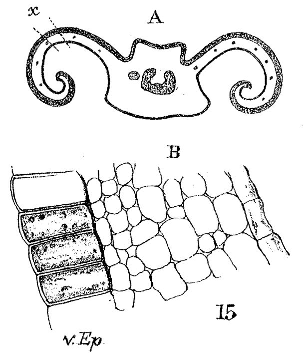

11

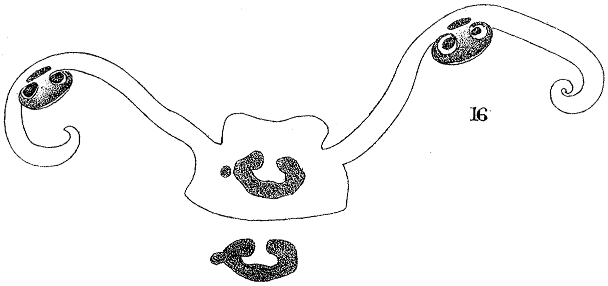
12

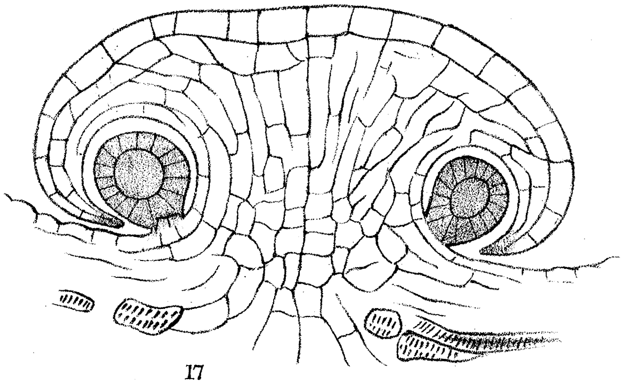


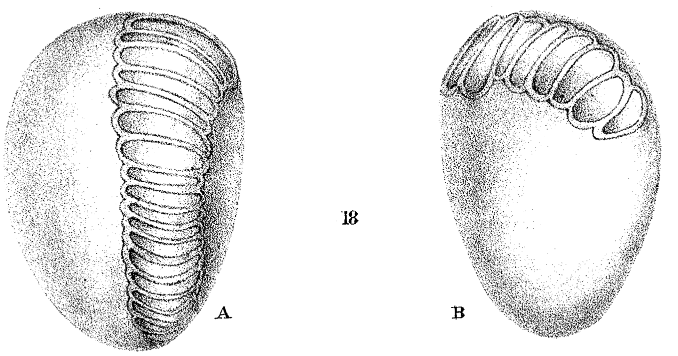

13

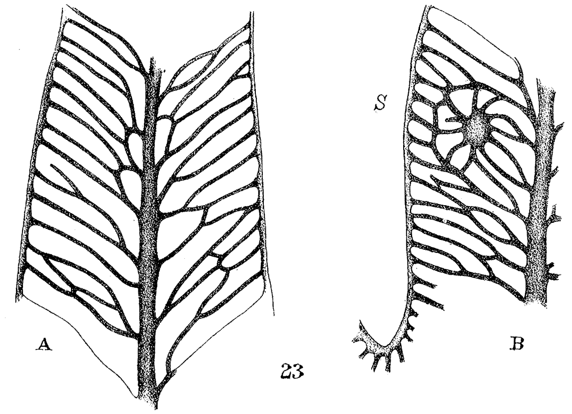

14

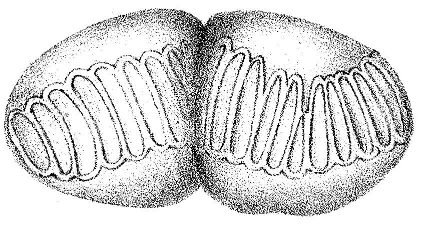

15

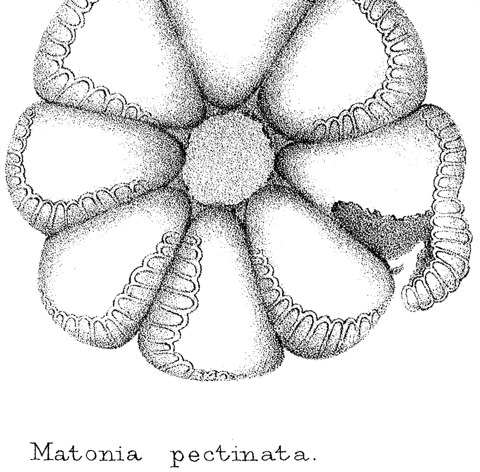

16

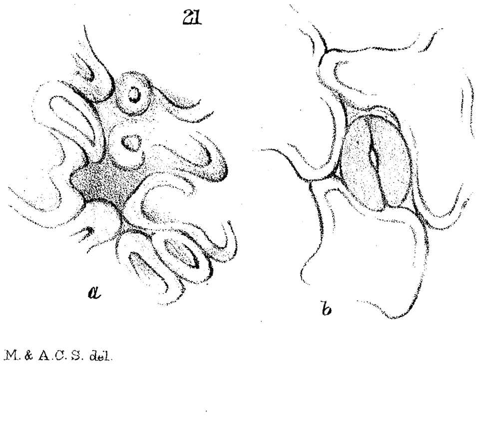

17

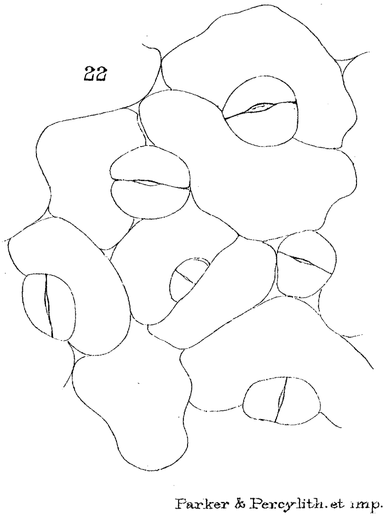

18


23


19


20

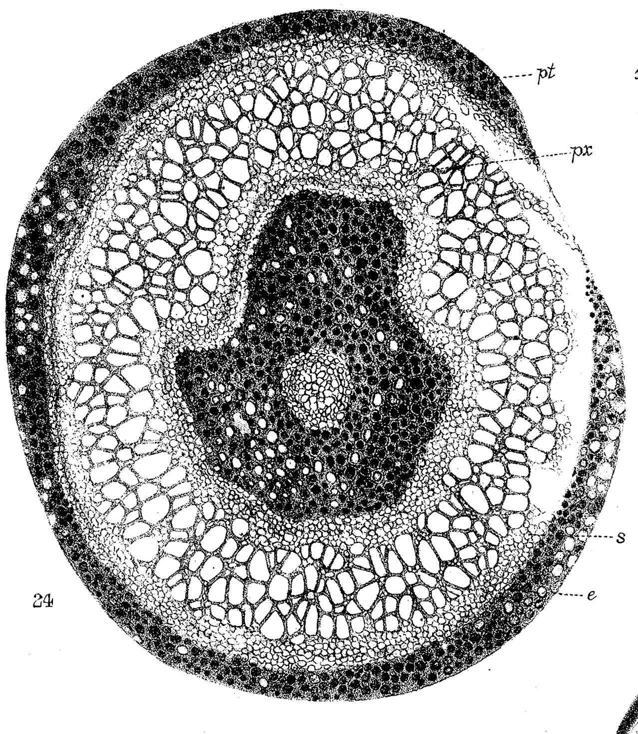

21


22

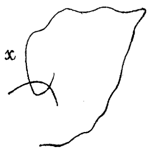
M. & A.C.S. del.

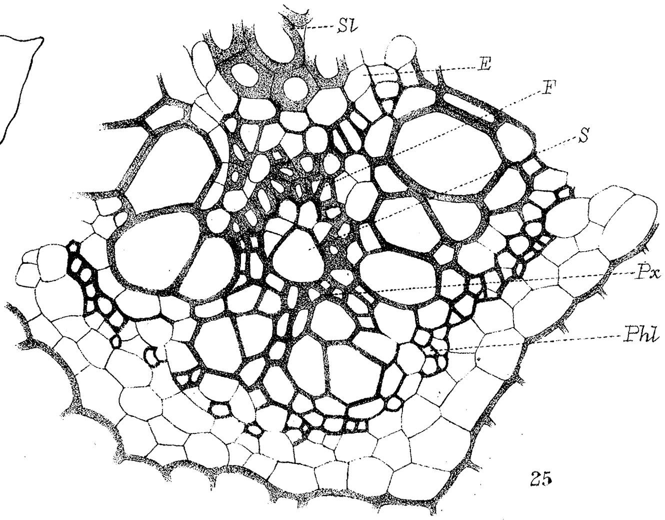
Parker & Percy lith. et imp.

Matonia pectinata.



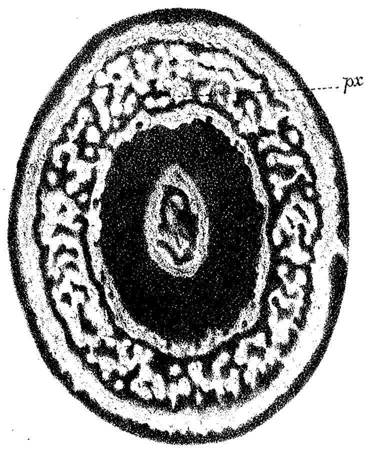
24

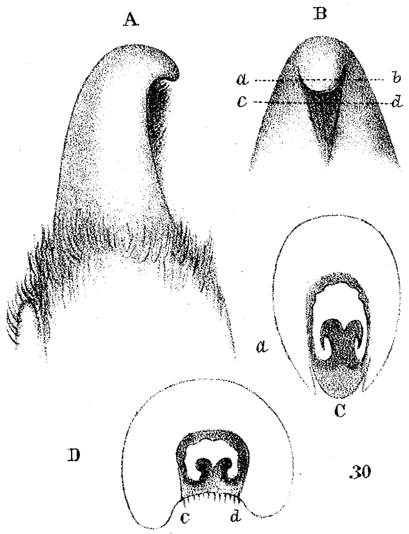




25

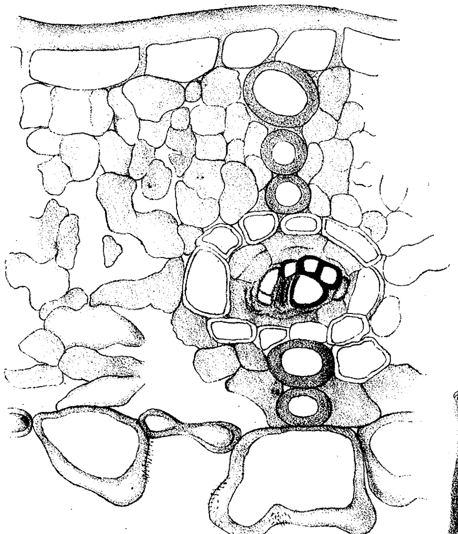
28



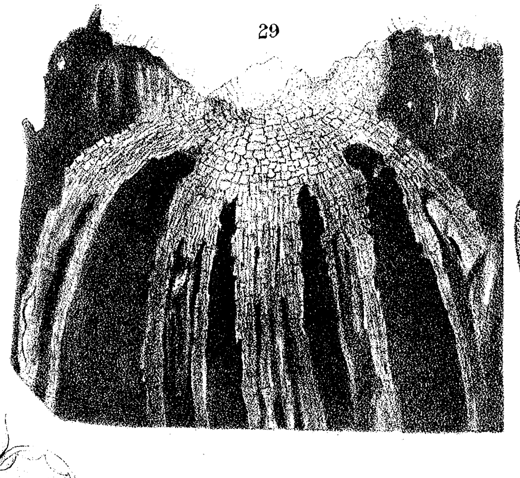


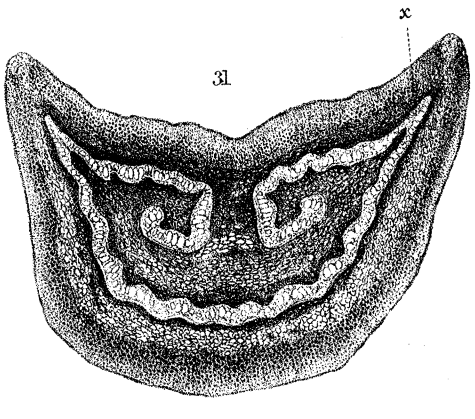
30

26



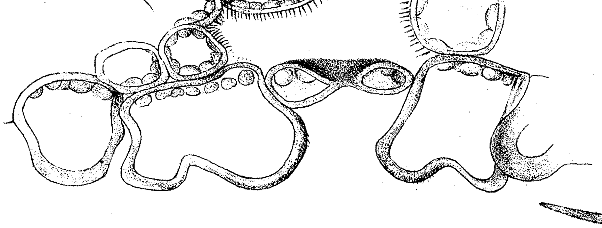
29





31

27



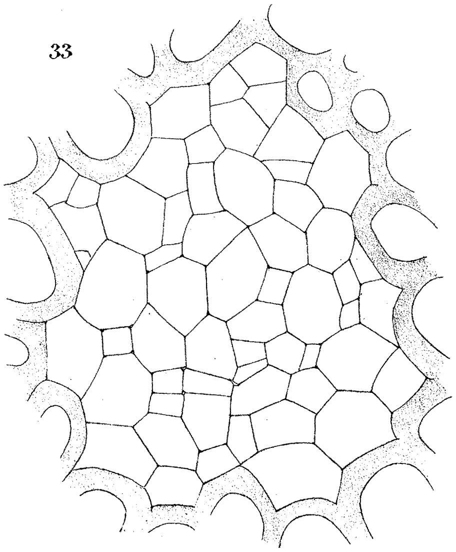
32

A.C.S. del.
W. Tams photo.

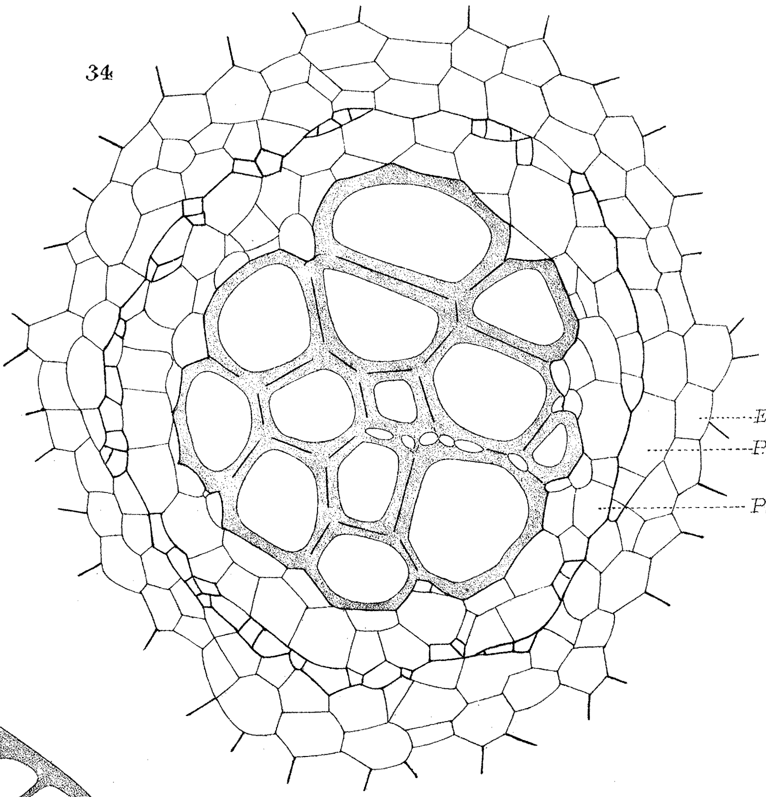
Parker & Percy lith. et imp.

Matonia pectinata.

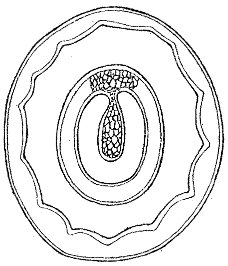
33



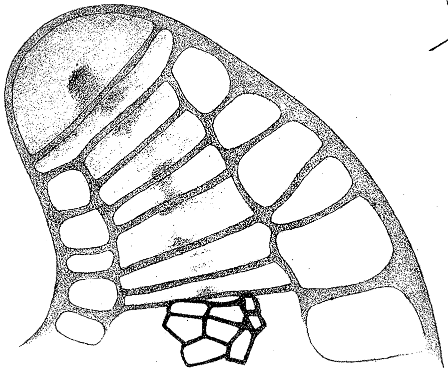
34



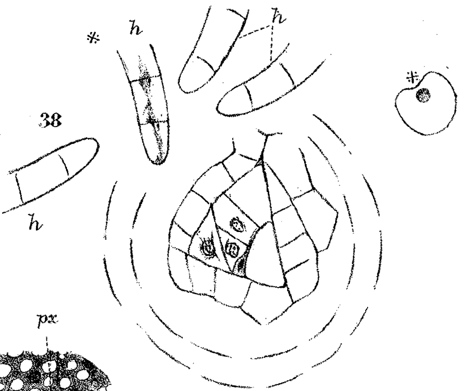
35



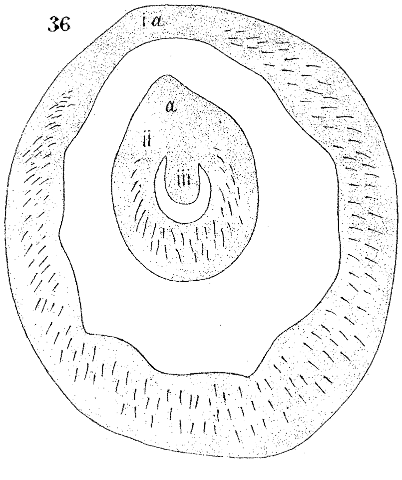
40



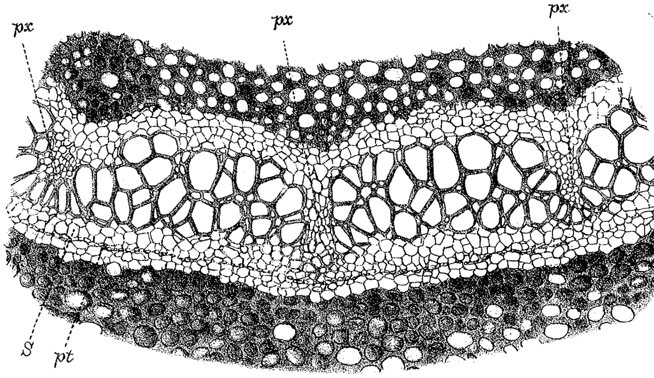
38



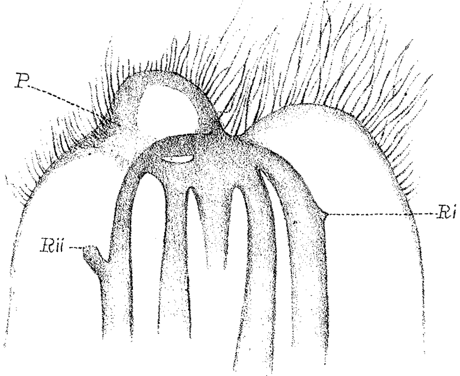
36



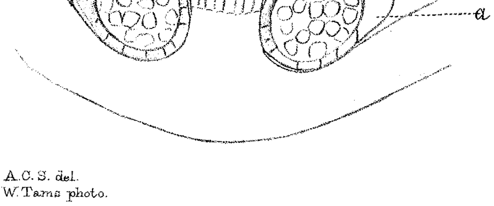
37



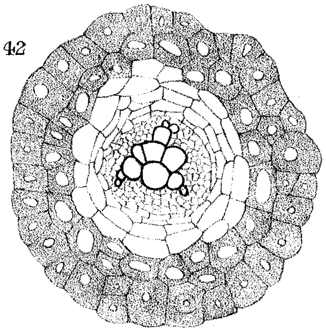
39



41



42



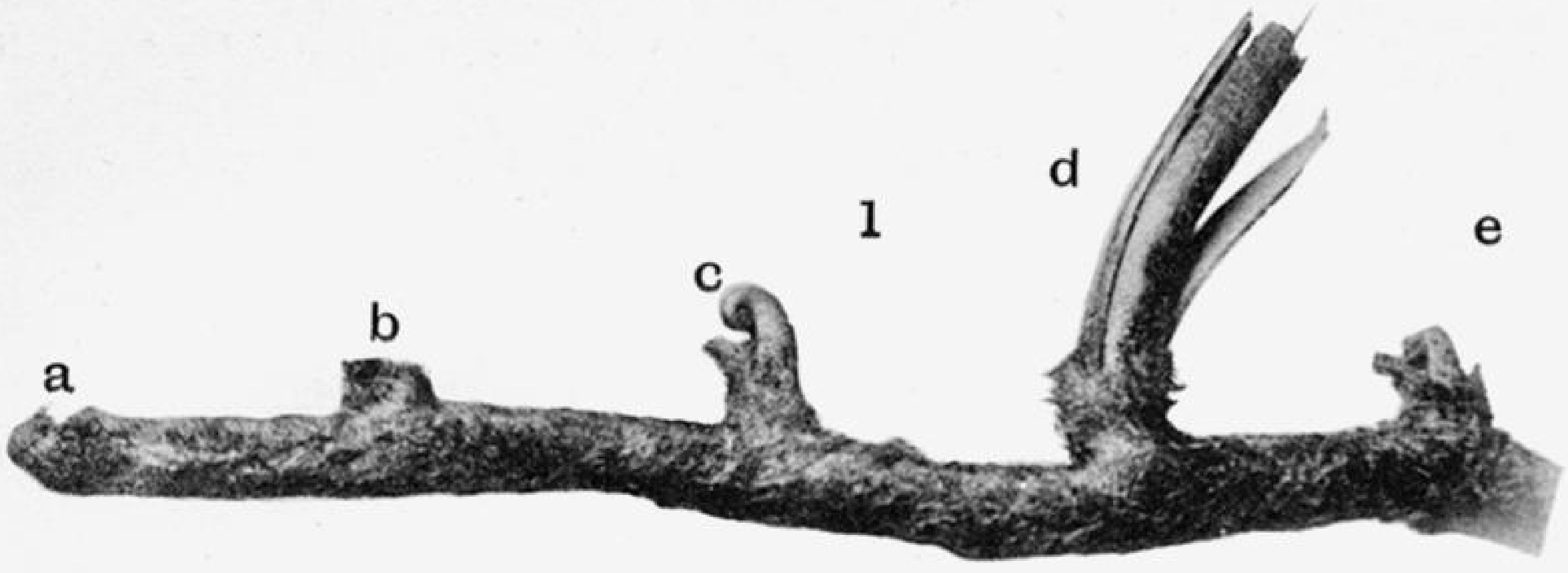
A. C. S. del.
W. Tams photo.

Parker & Percy lith. et imp.

Matonia pectinata.

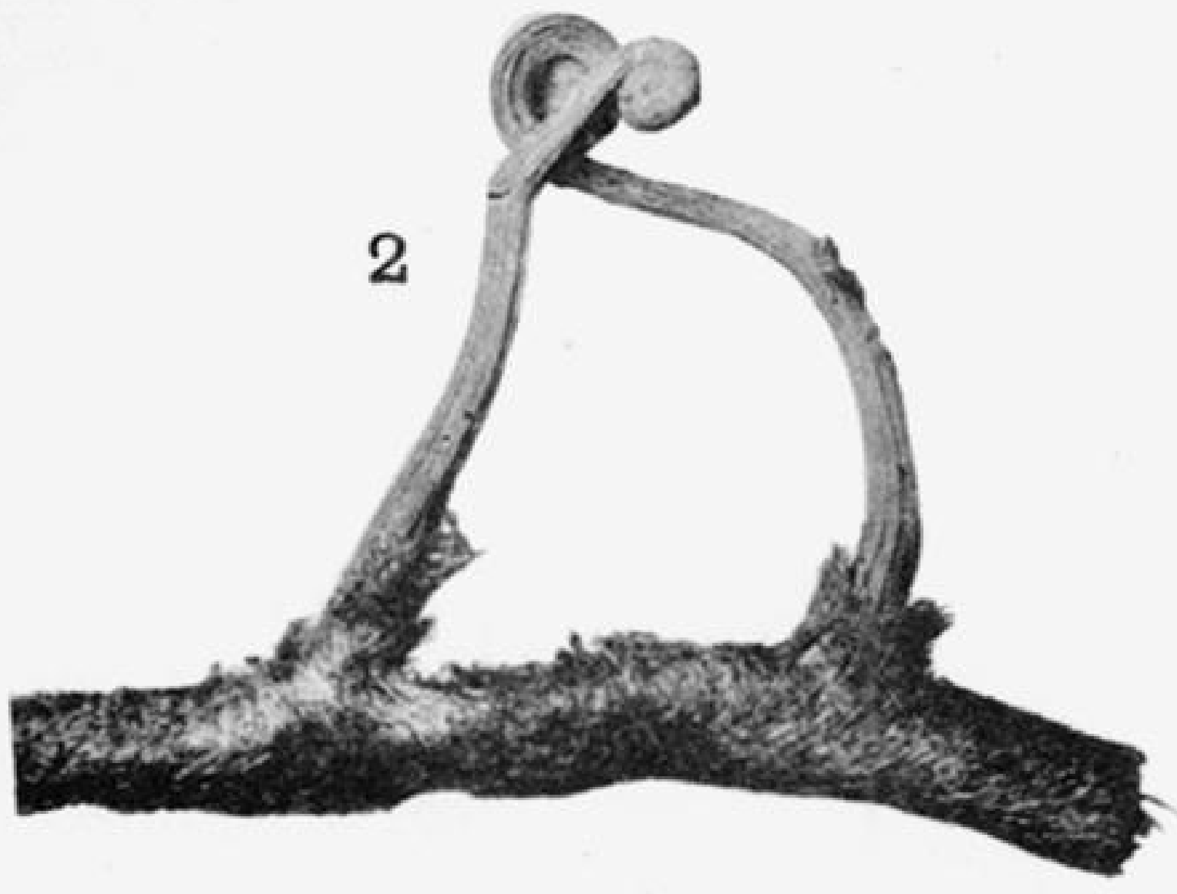
Fig. 8.

Laccopteris elegans (Presl). From a specimen (No. 500) in the British Museum, Lower Keuper, Bayreuth. Frond nat. size; pinnule × 3. (Drawn by Miss G. M. Woodward.)

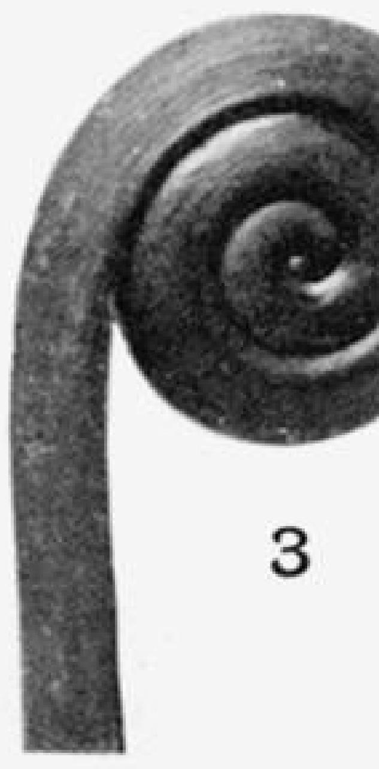


1

8

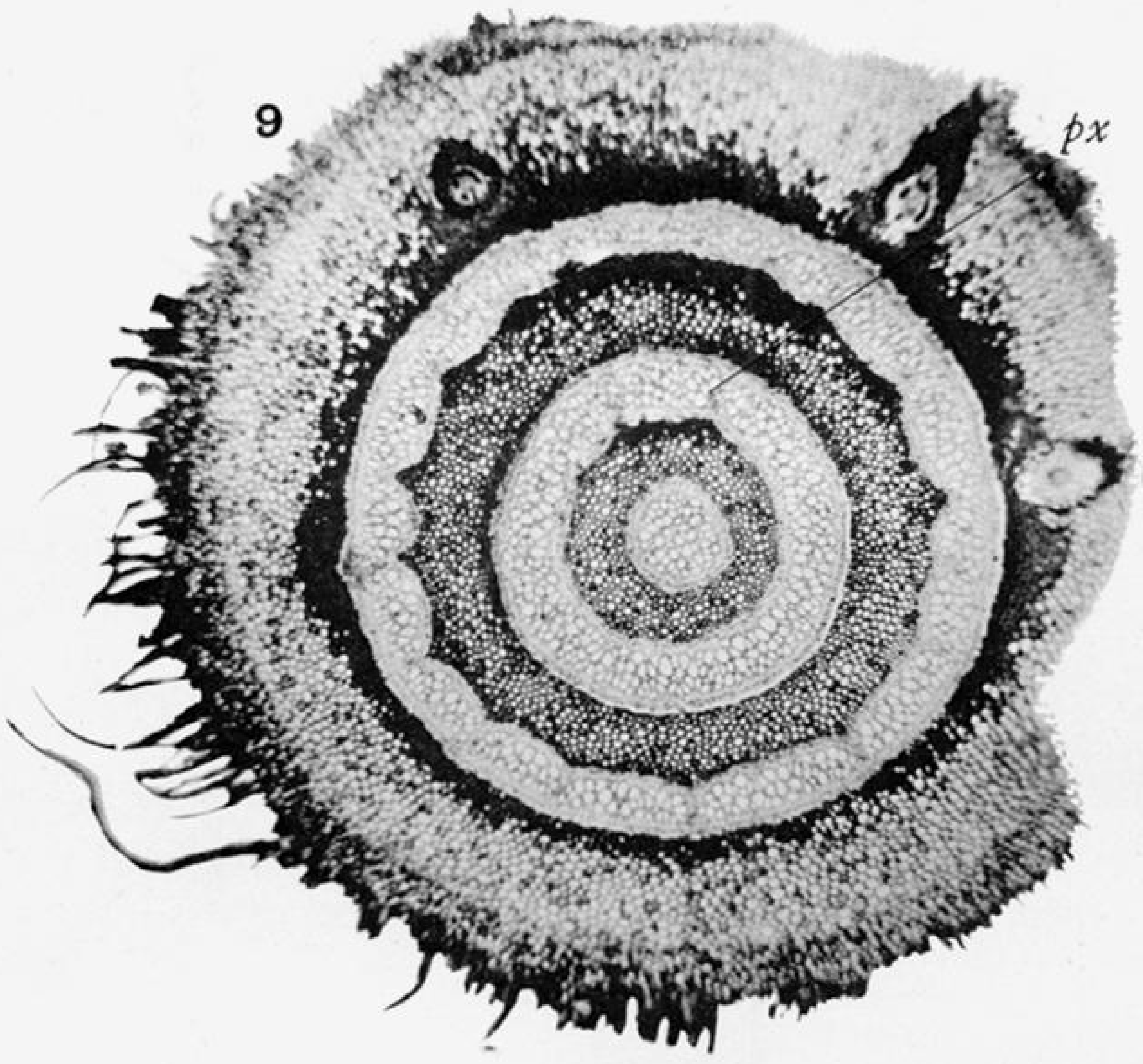


2



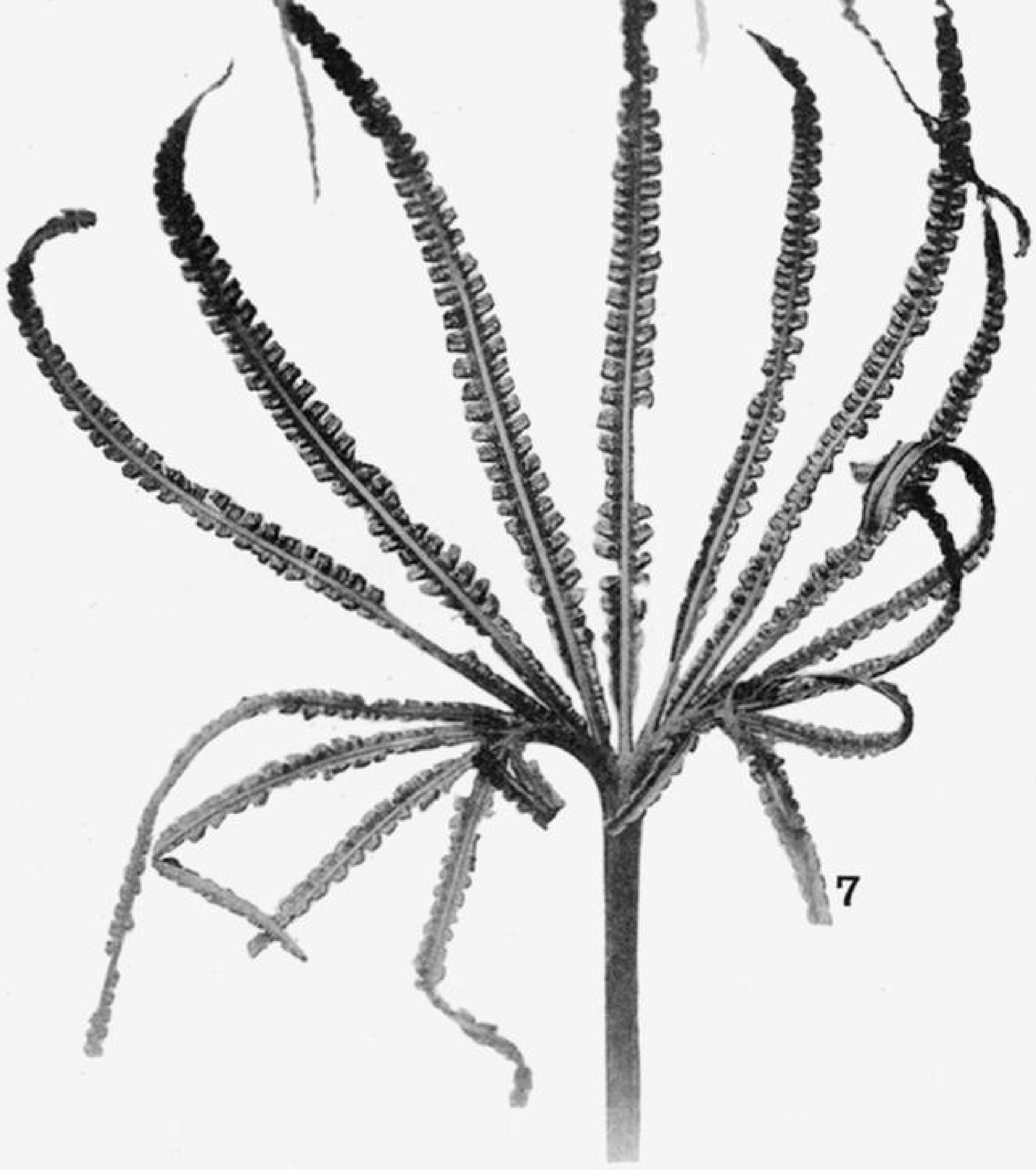
3

4



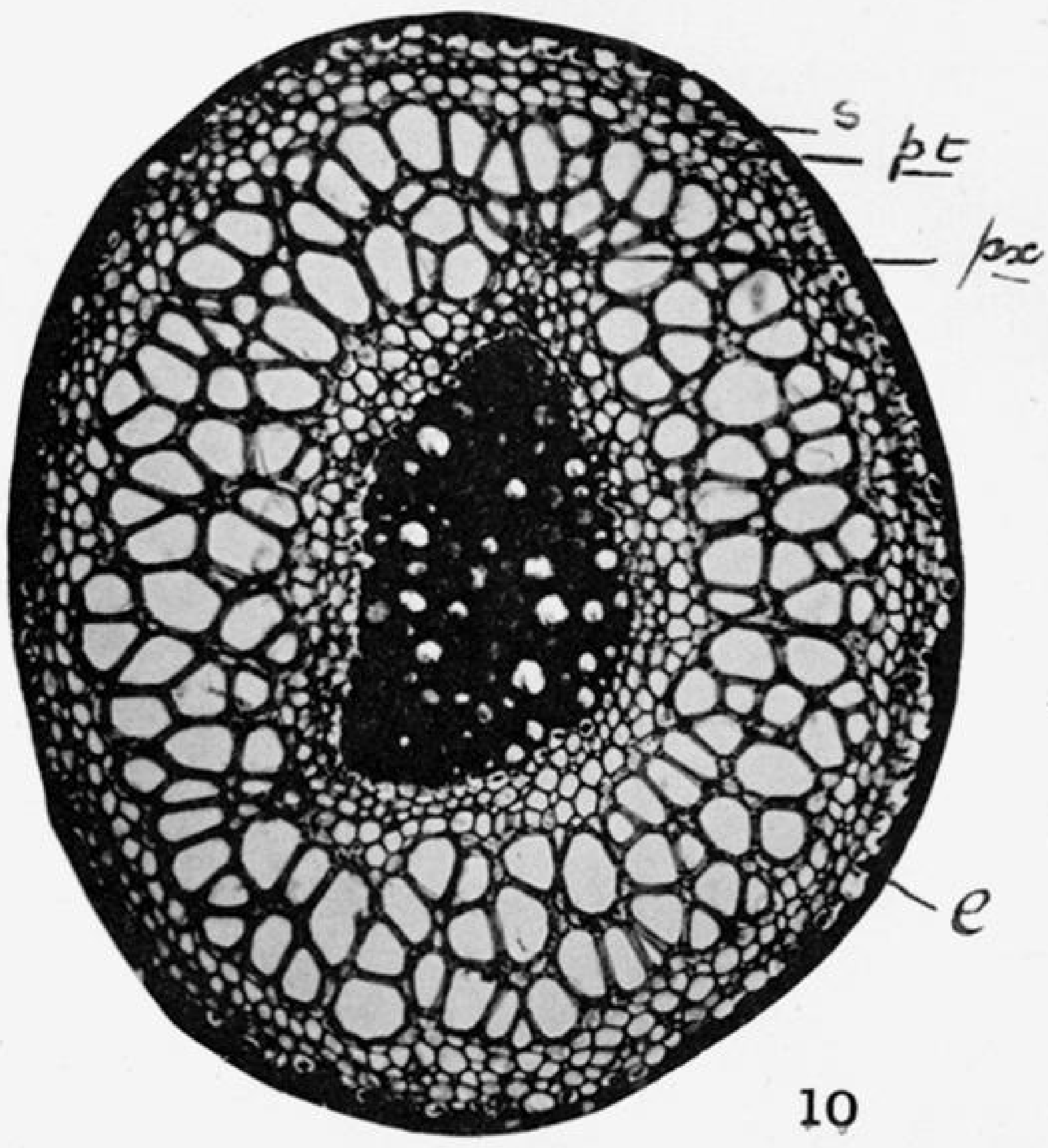
9

5

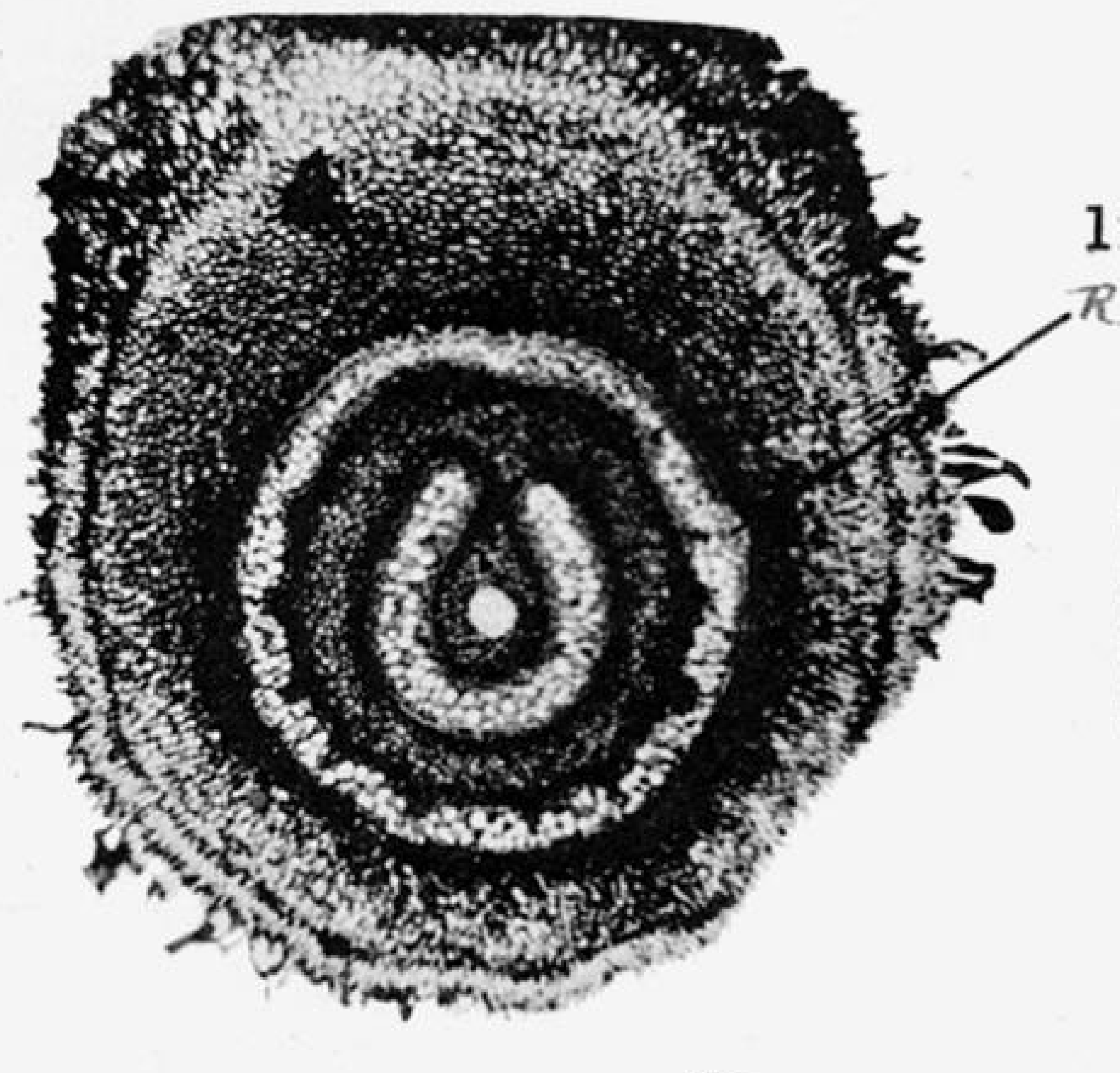


7

6



10



11

12

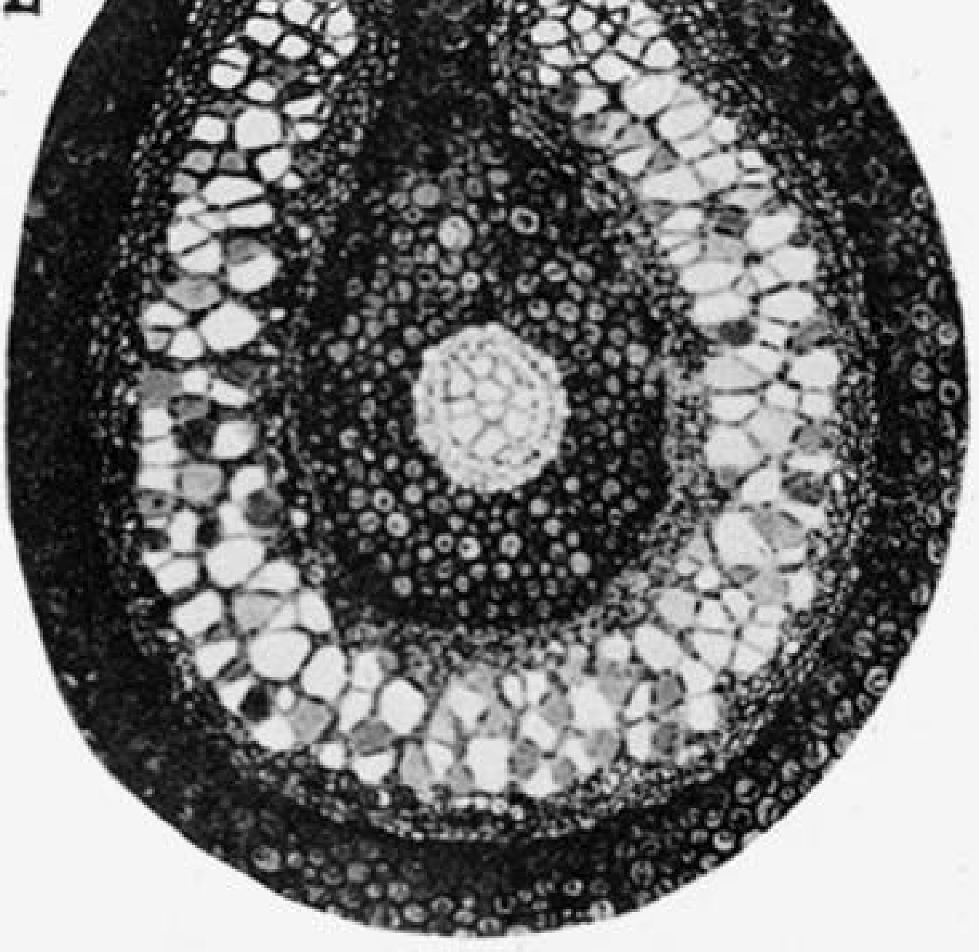


PLATE 17.

Matonia pectinata, R. Br.

Fig. 1. Piece of rhizome showing the apex and young fronds, *a–e* (nat. size).

Fig. 2. Piece of rhizome with two young fronds (nat. size).

Figs. 3–6. Stages in the development of a frond (nat. size).

Fig. 7. Frond partially expanded (nat. size).

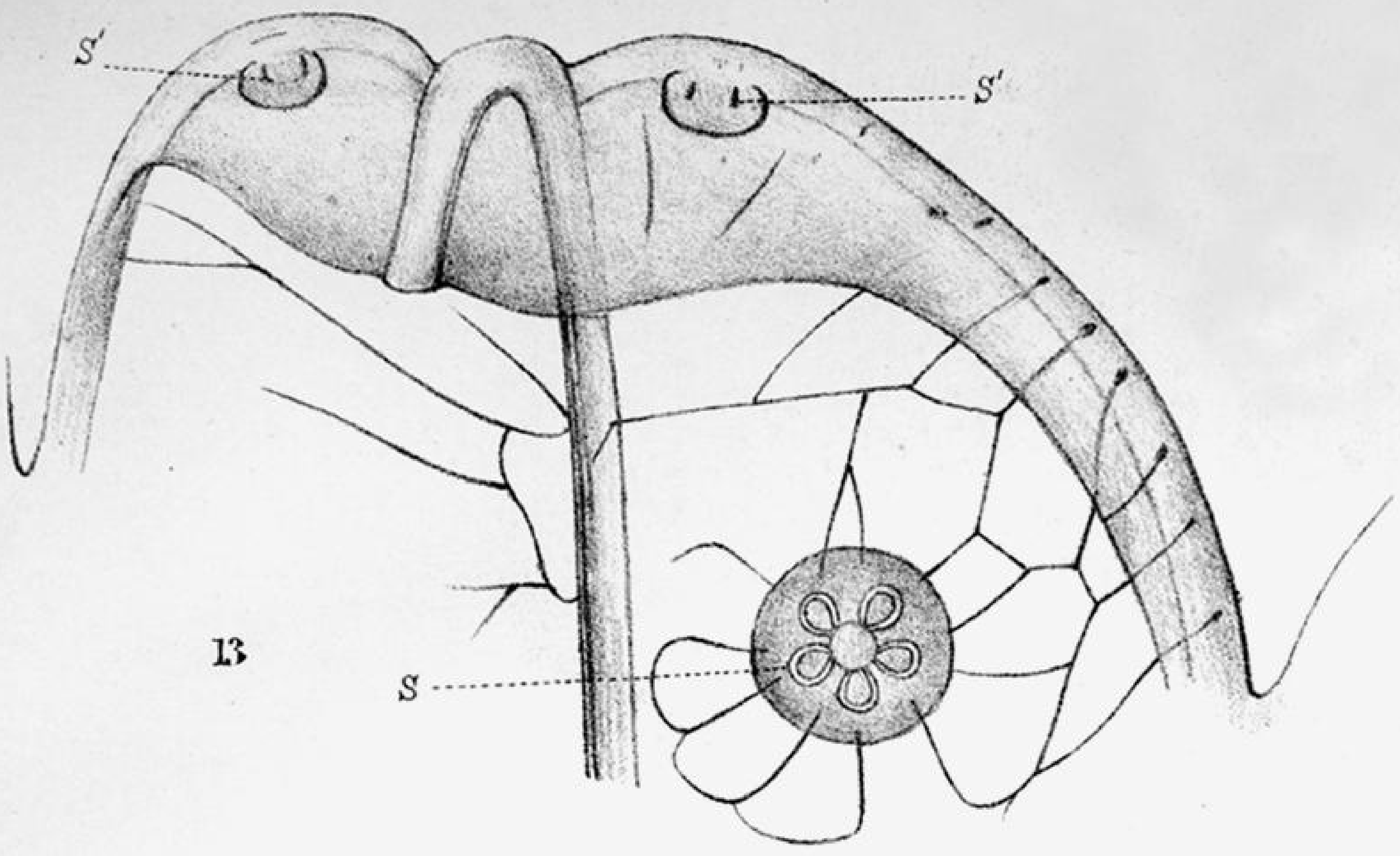
Fig. 8. Transverse section of rhizome showing two annular steles. (× 15.)

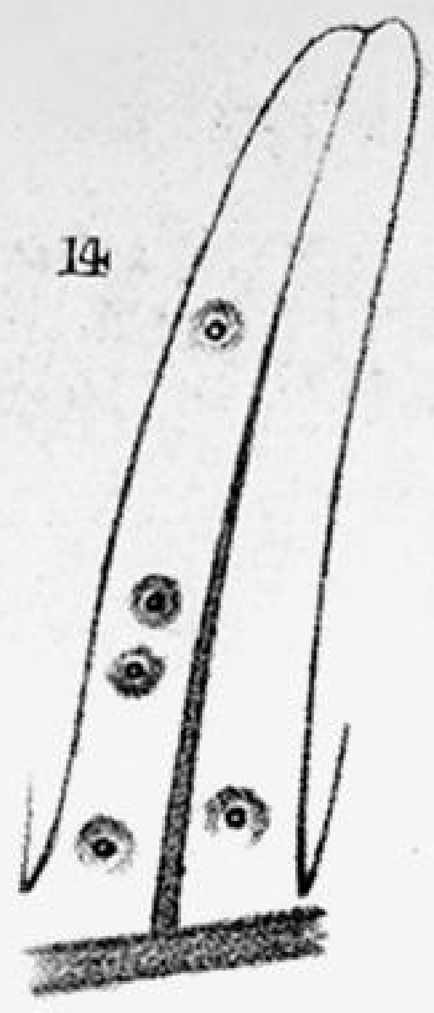
Fig. 9. Transverse section showing three steles, and four roots in different stages of growth. *px.*, protoxylem of the second annular stele. (× 15.)

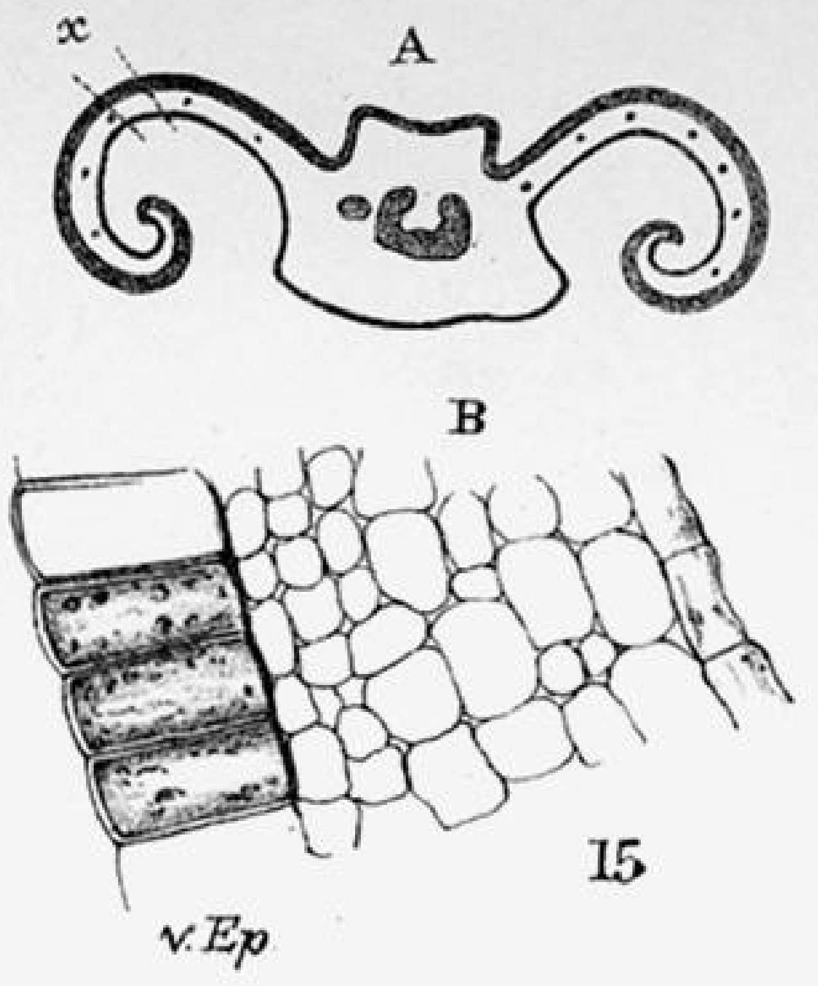
Fig. 10. The inner stele of fig. 8. *px*, protoxylem; *S*, sieve-tubes; *pt*, protophloem; *e*, endodermis. (× 60.)

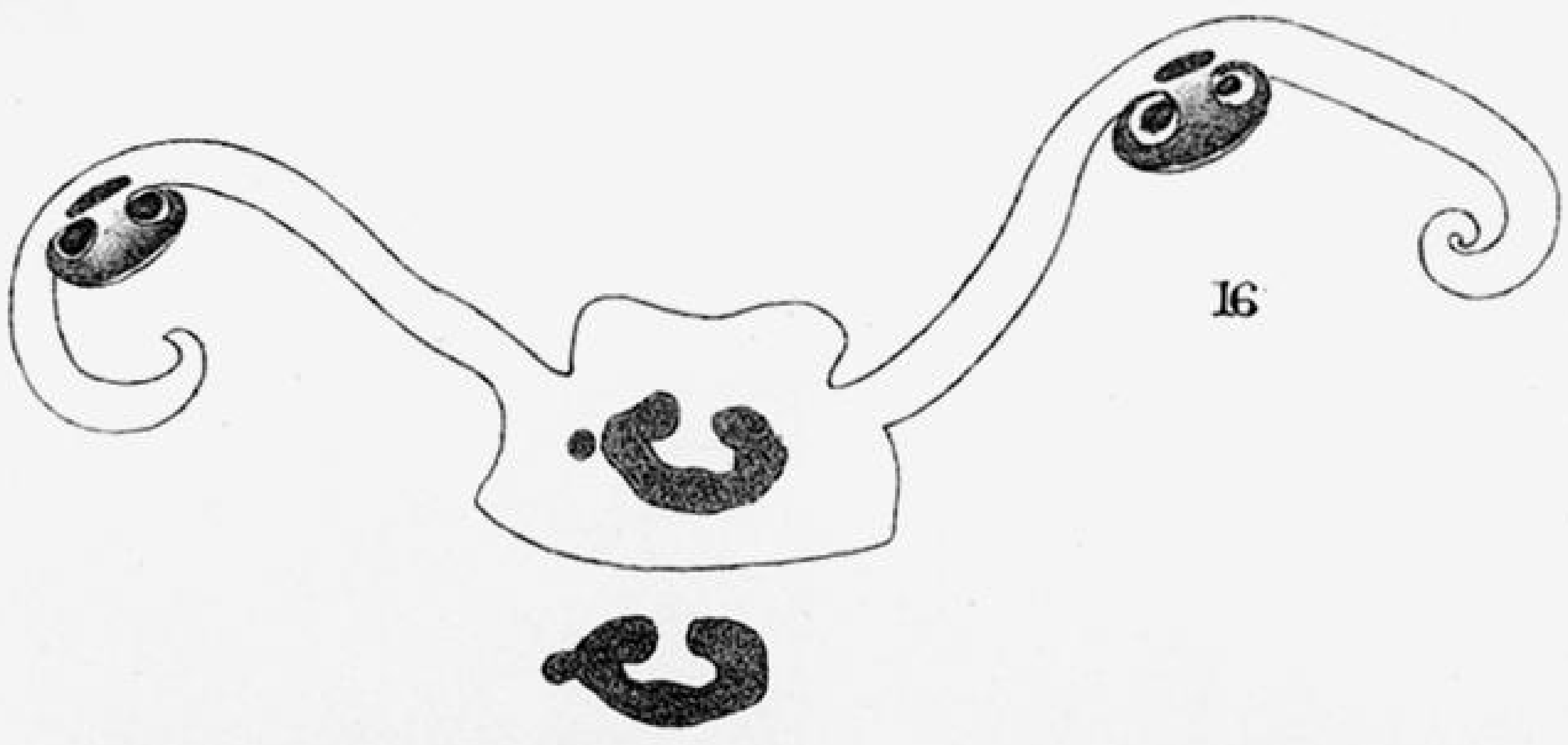
Fig. 11. Transverse section of rhizome immediately in front of a leaf, showing three steles, the second annular stele open at the top. R, young root. (× 15.)

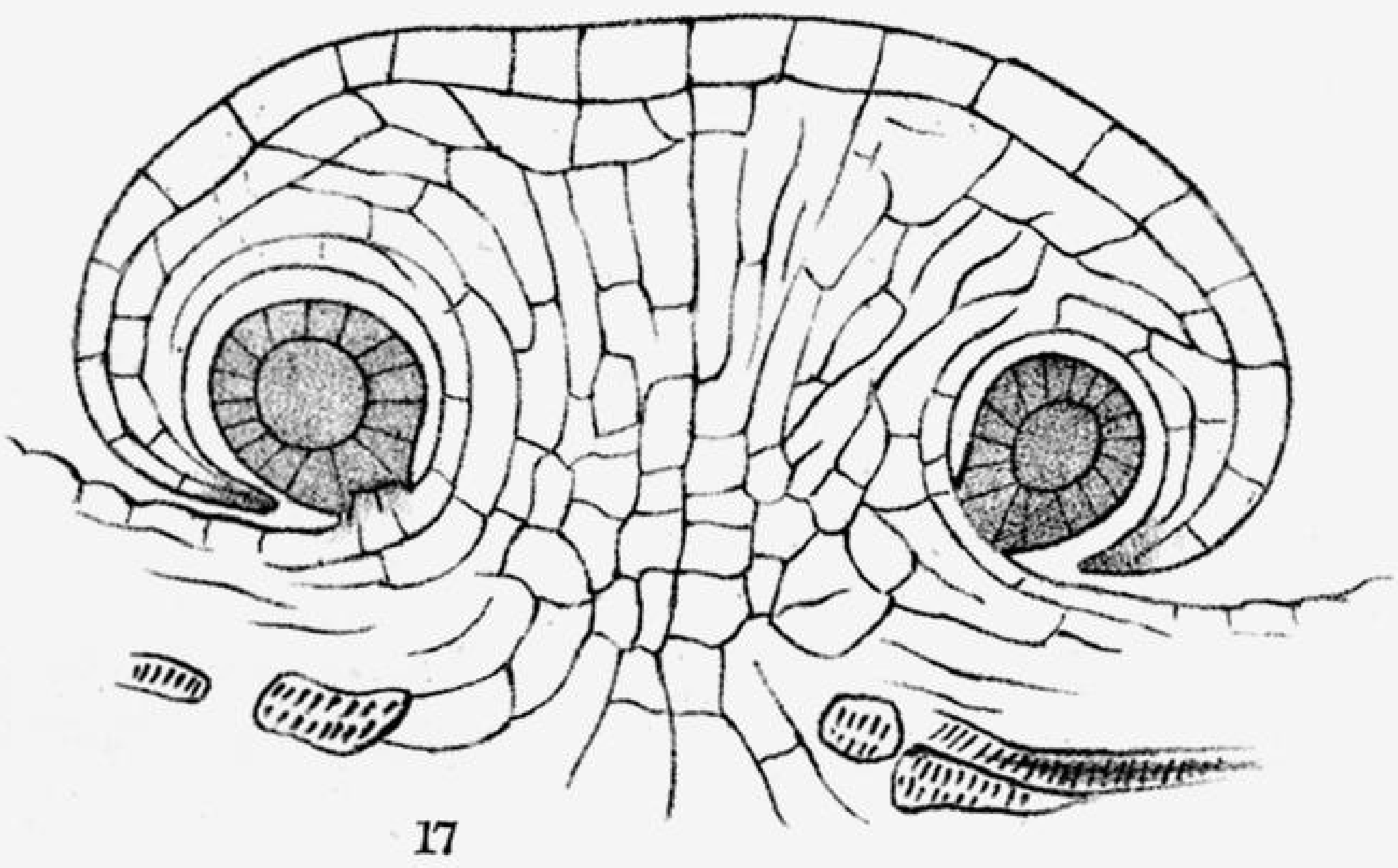
Fig. 12. Portion of fig. 11, more highly magnified. (× 40.)

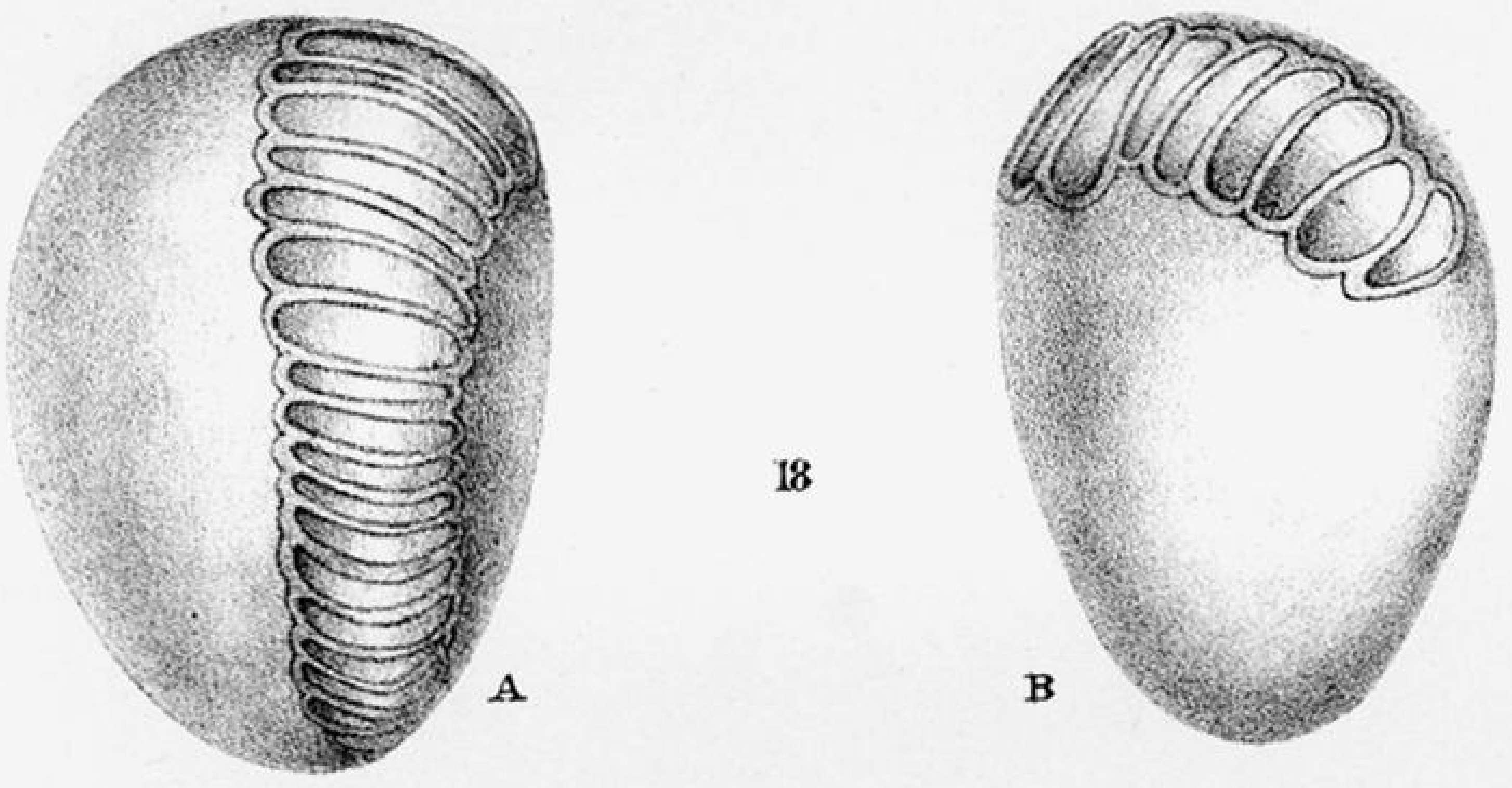


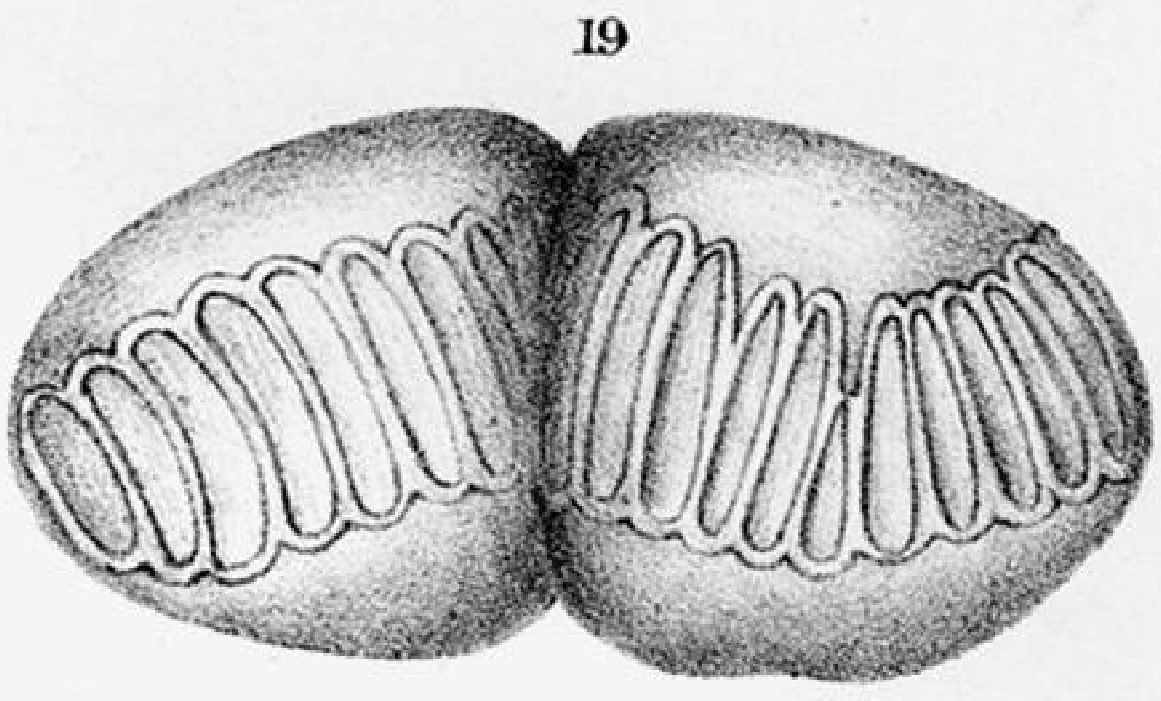


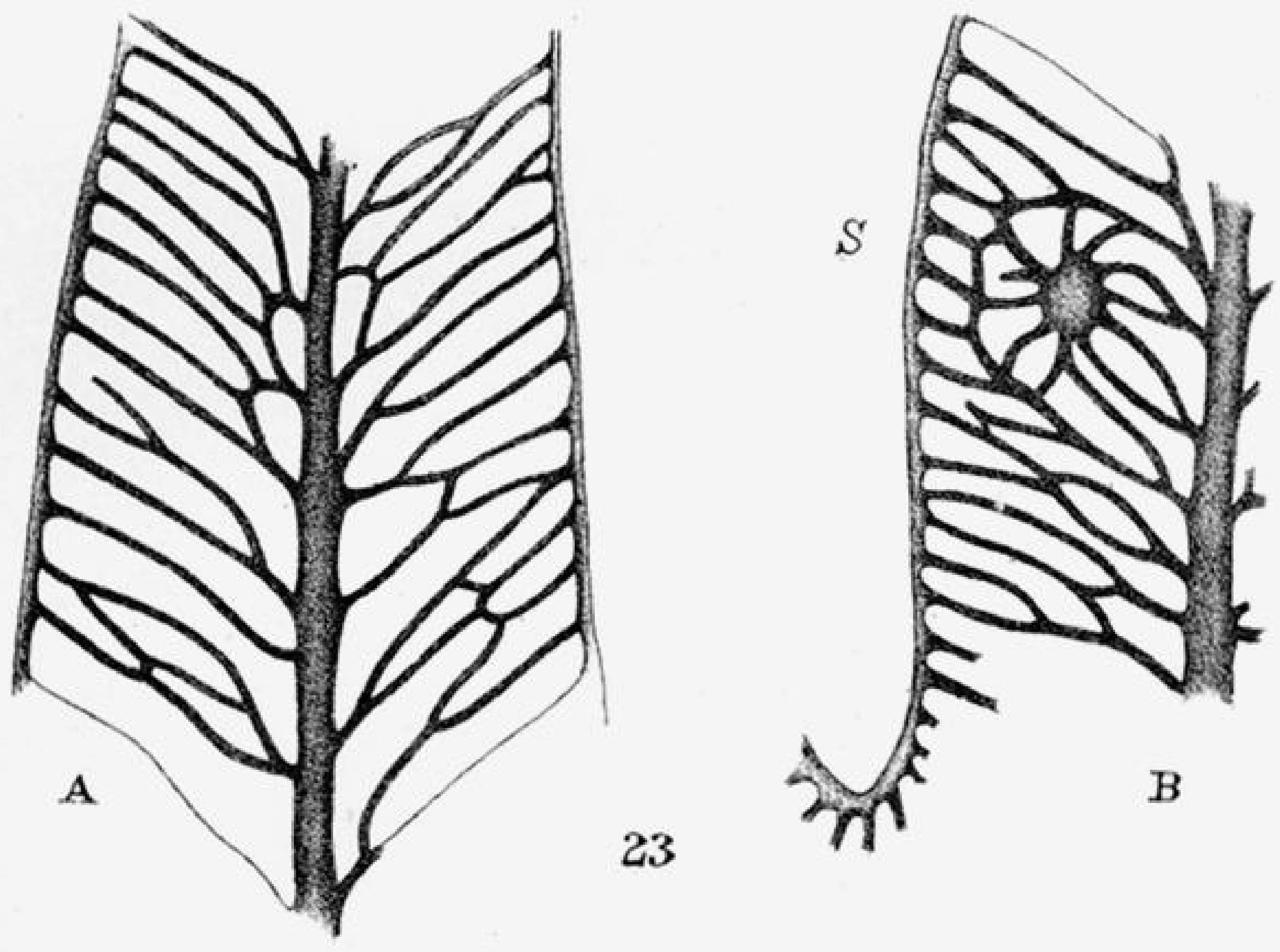


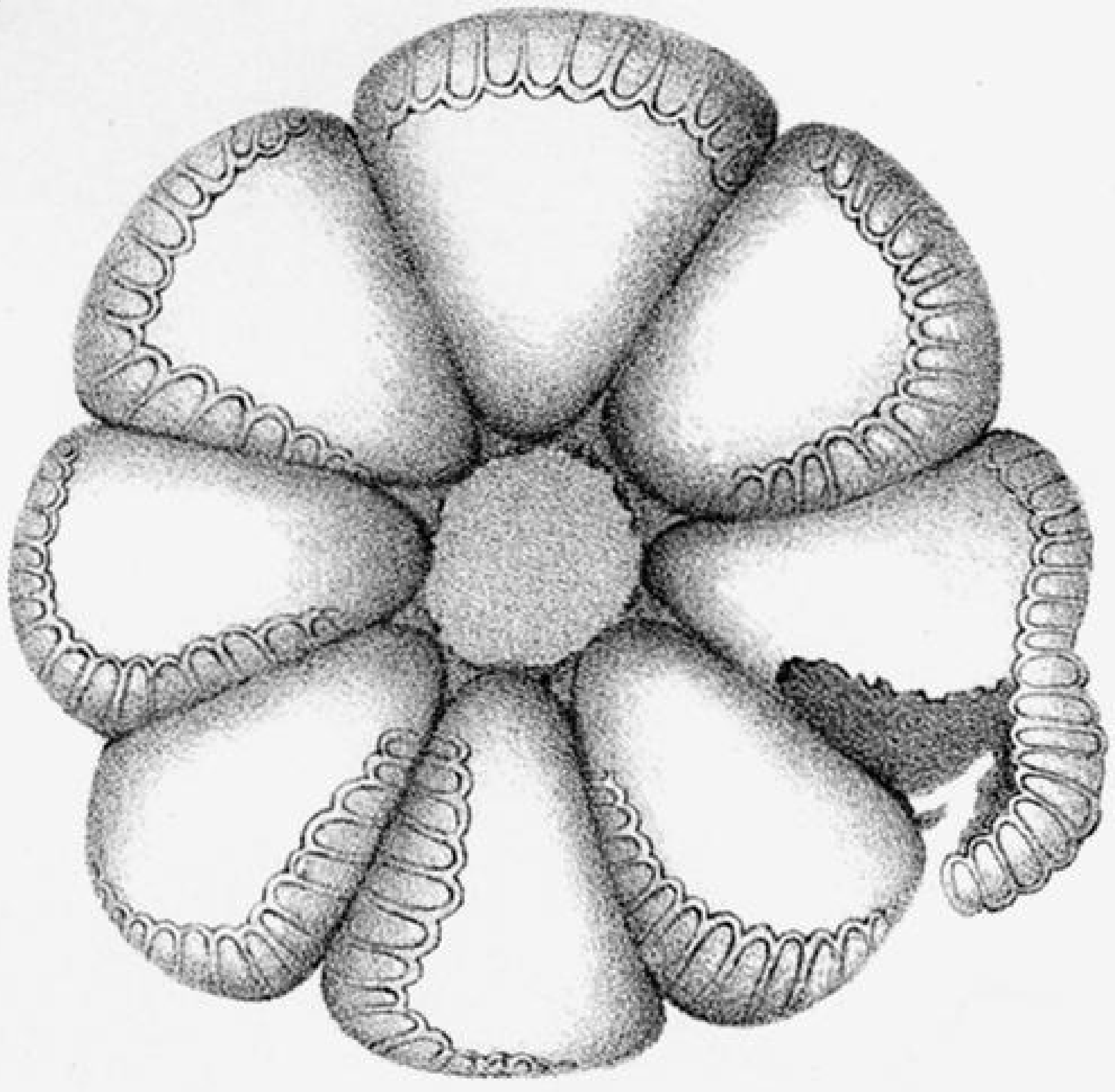


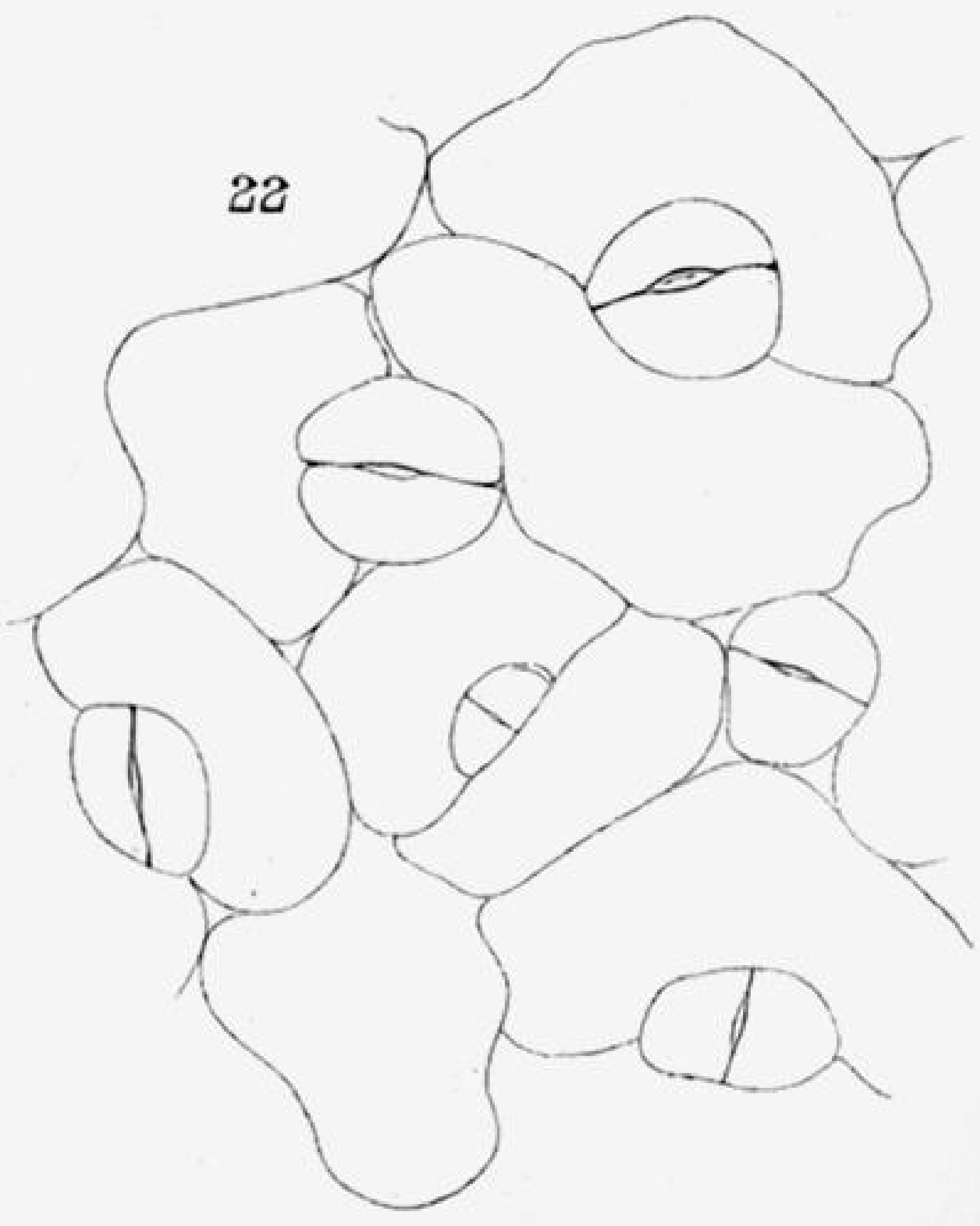












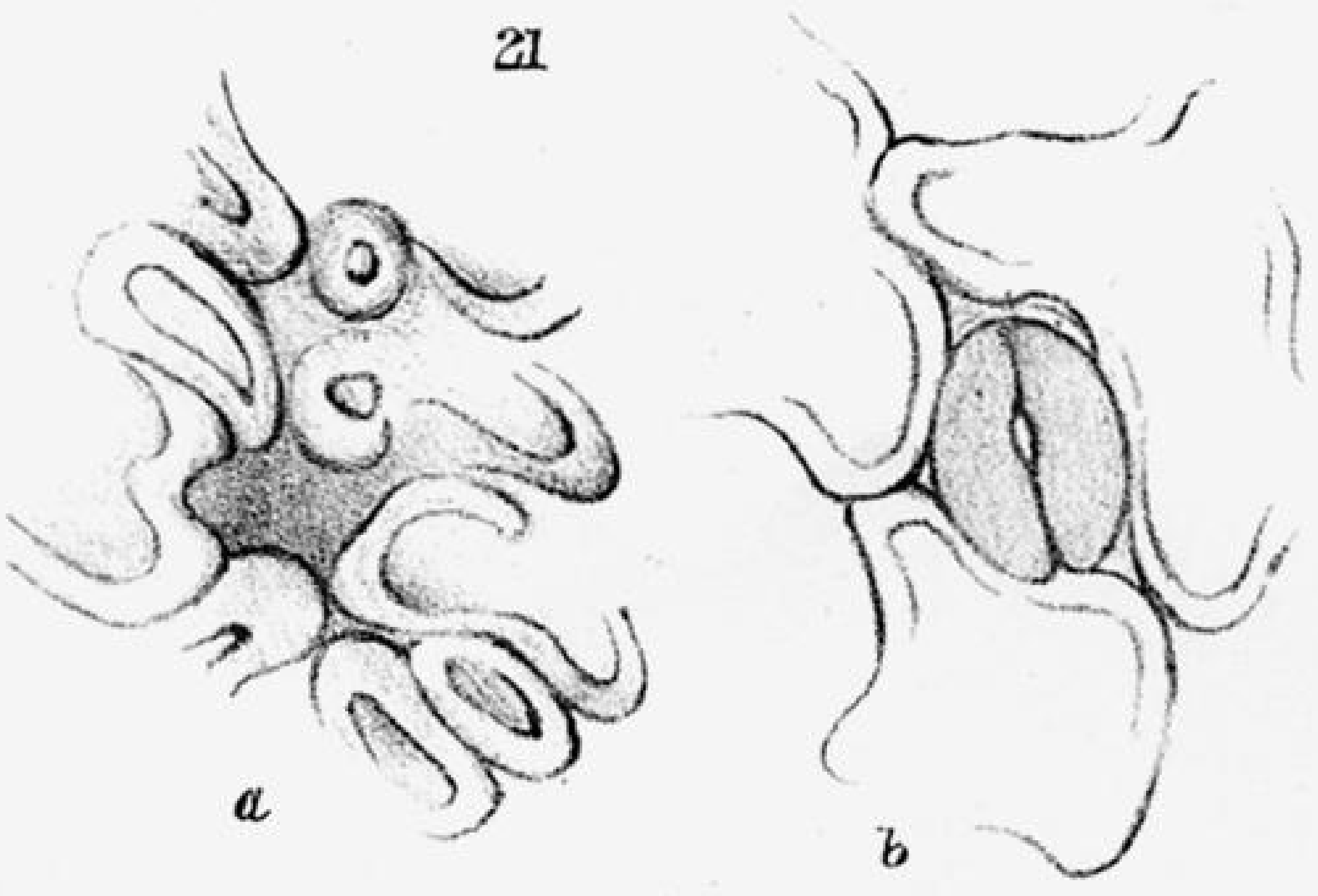


PLATE 18.

Matonia pectinata, R. Br.

Fig. 13. The inner face of a young pinnule. *s*, *s'*, *s'*, sori. (× 16.)

Fig. 14. A single mature pinnule, with five circular depressions, from which sori have become detached (slightly enlarged).

Fig. 15. A, diagrammatic transverse section of a young pinnule; B, portion of the lamina of A (*x*). *Ep*, upper epidermis. (× 16.)

Fig. 16. Diagrammatic transverse section of an older pinnule, with two sori.

Fig. 17. A young sorus in vertical section, showing two immature sporangia, the large central receptacle and the circular indusium; a few short scalariform tracheids below the receptacle. (× 23.)

Fig. 18. A sporangium viewed from two opposite sides, A and B, to show the incomplete oblique annulus.

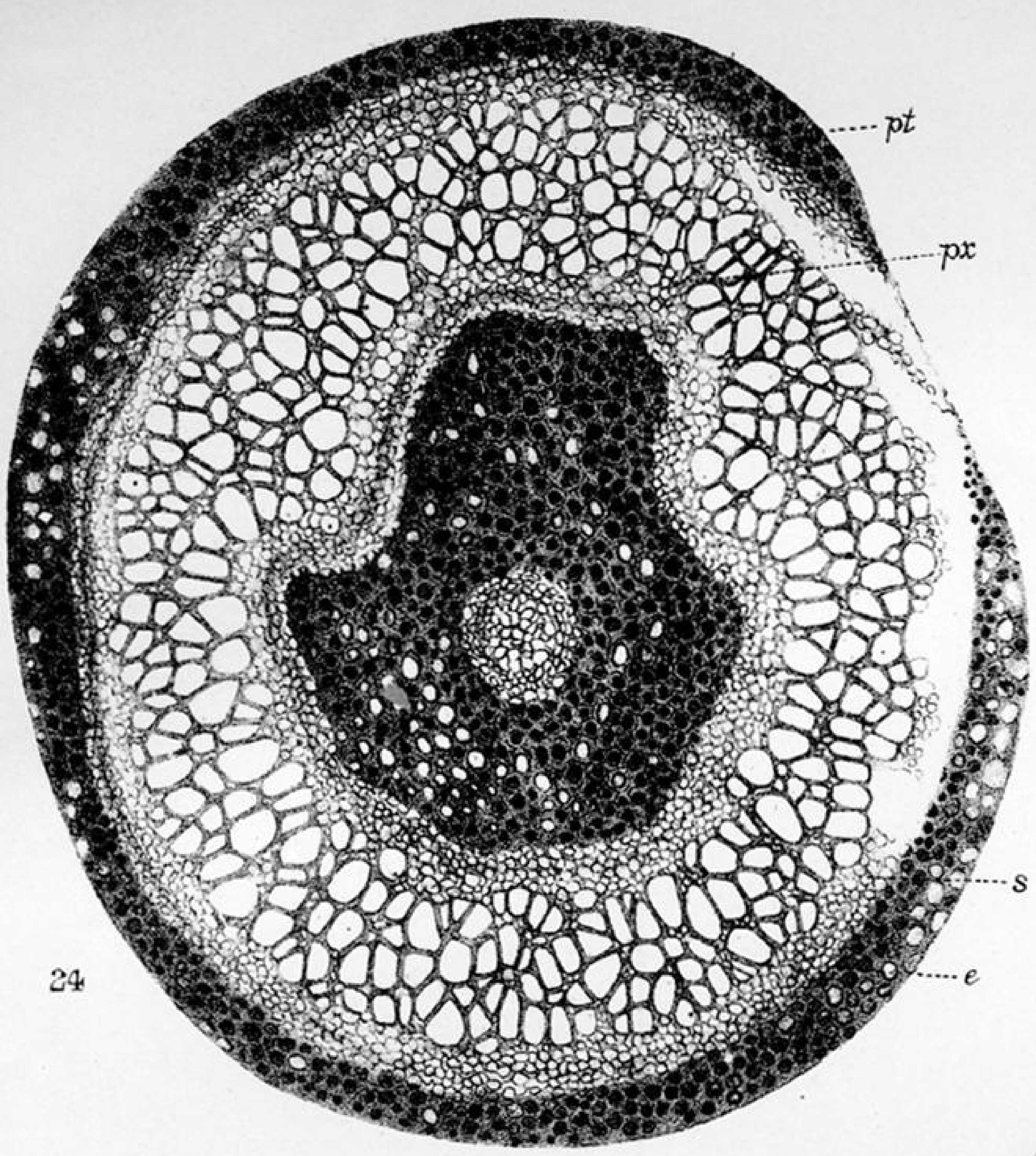
Fig. 19. Two sporangia as seen in side-view of a sorus.

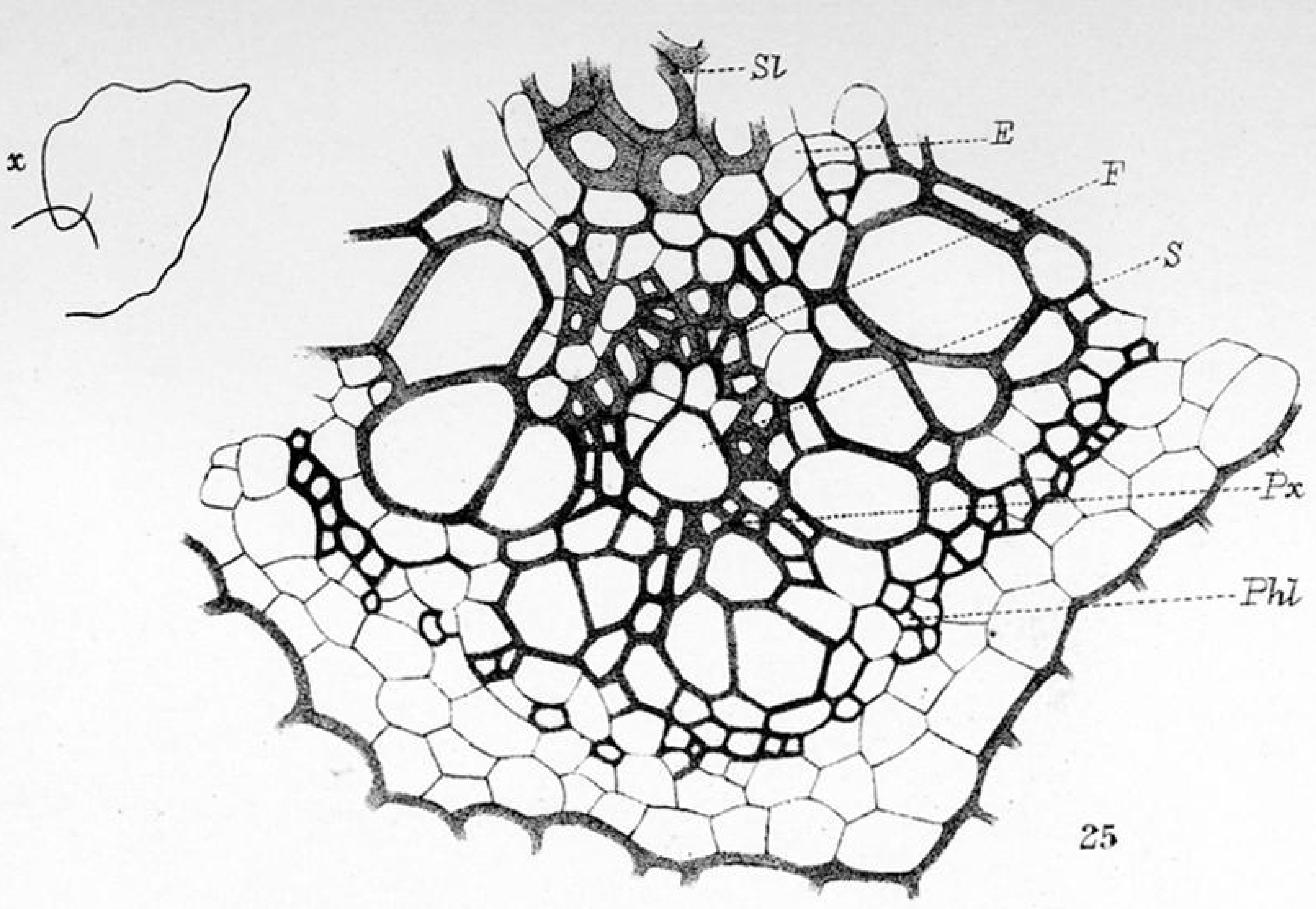
Fig. 20. A sorus from which the indusium has been naturally detached.

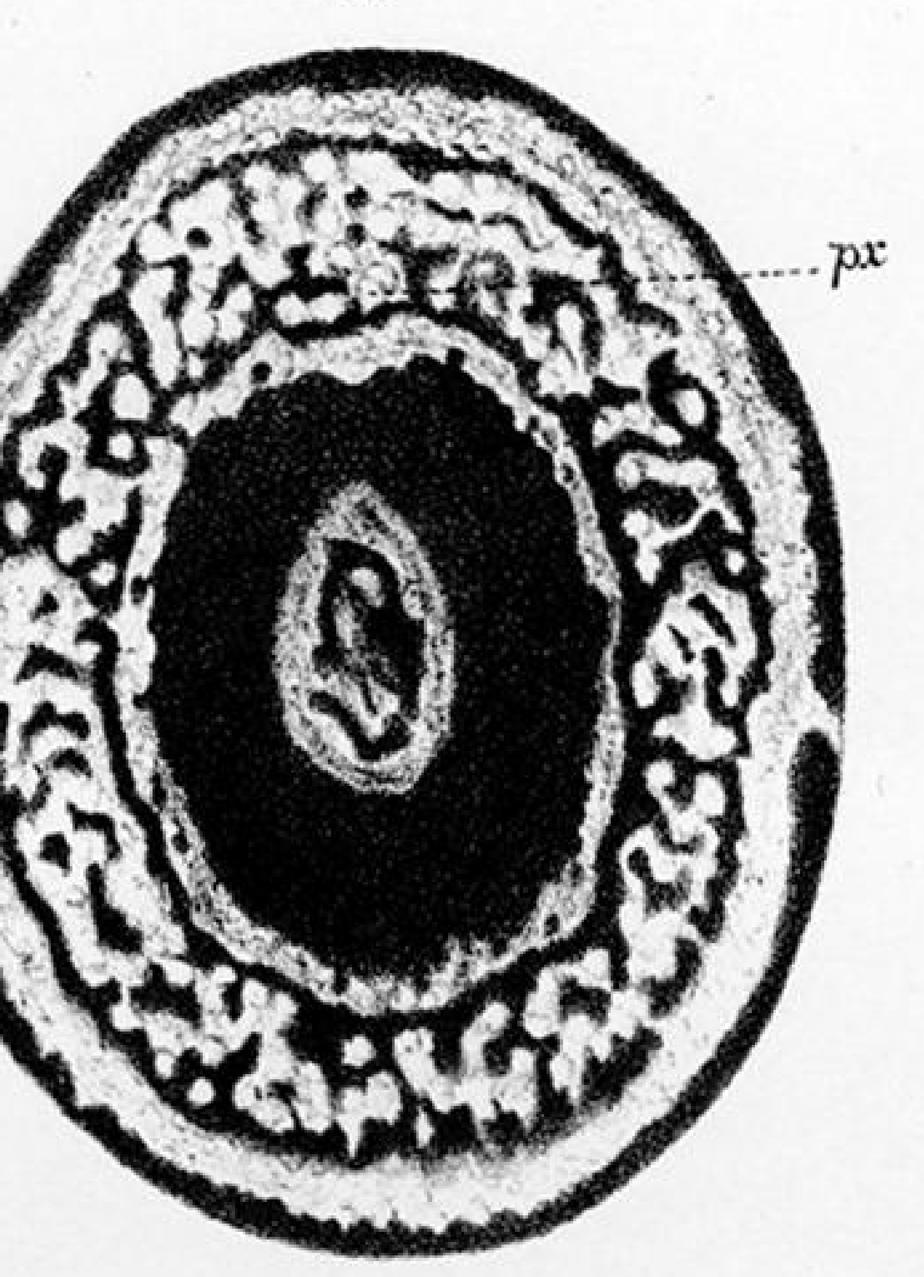
Fig. 21. A stoma in surface-view: *a*, the surface of the papillose lower epidermal cells in focus; *b*, the two guard-cells in focus. (× 240.)

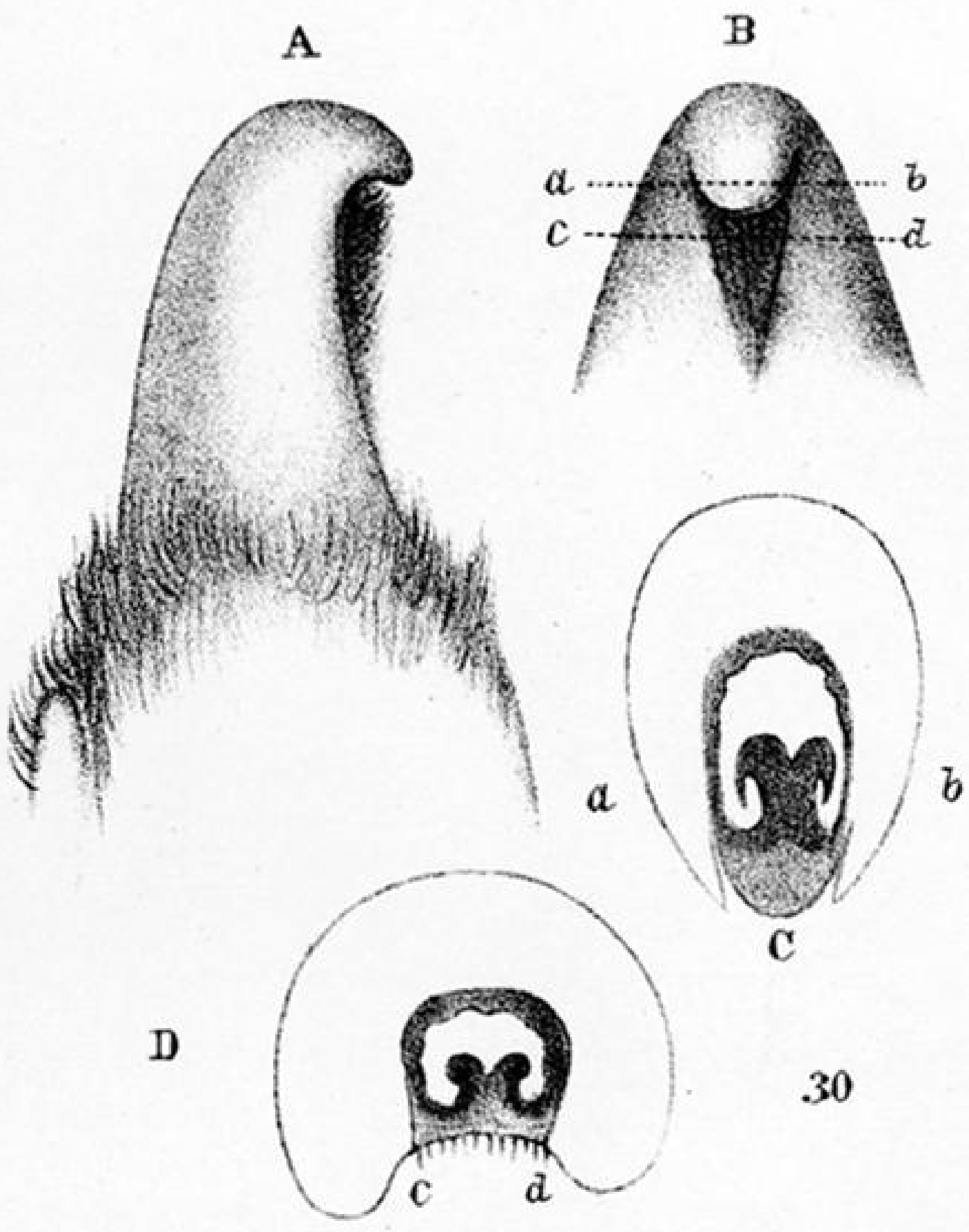
Fig. 22. Stomata in different stages of development as seen in surface-view of a young pinnule. (× 240.)

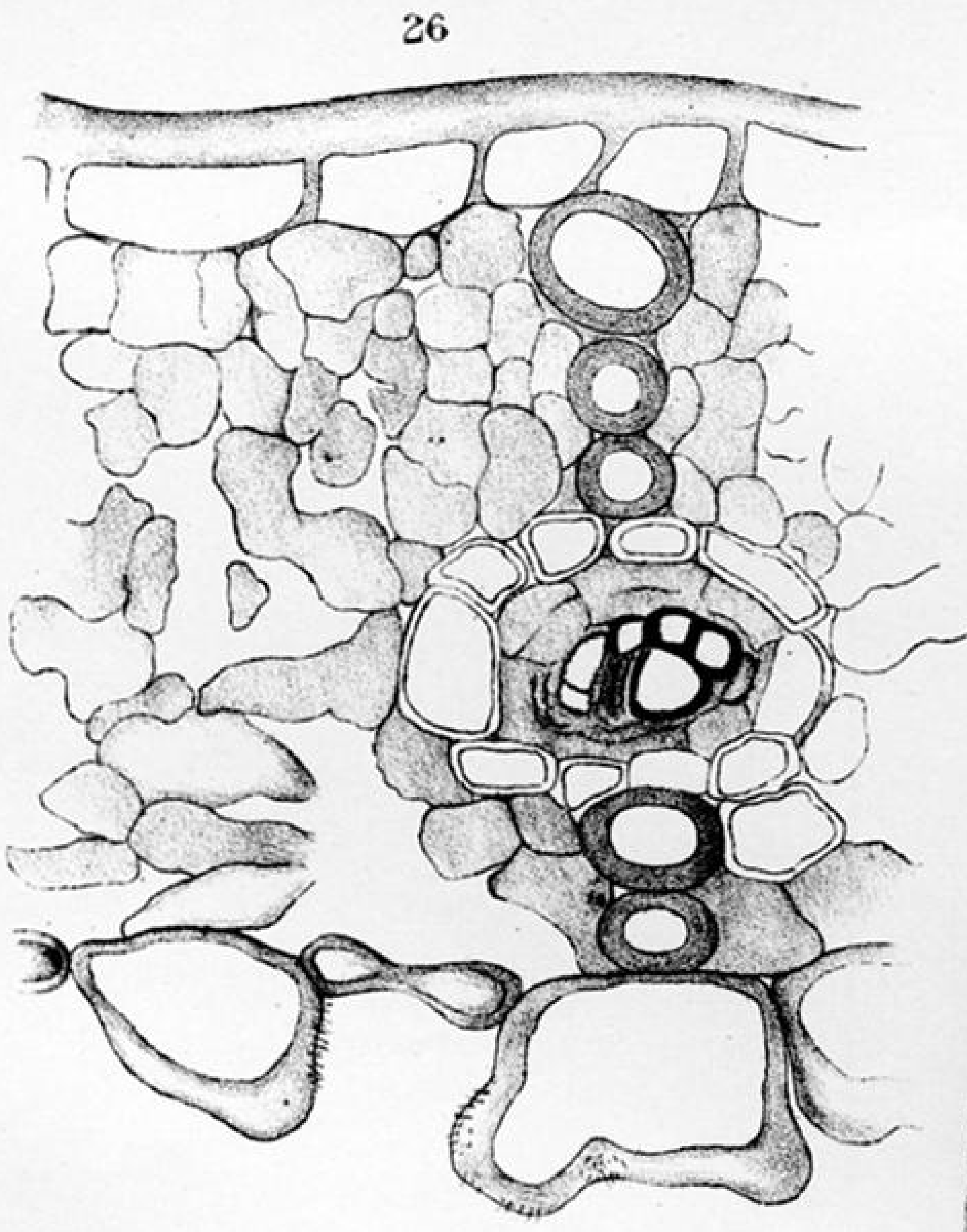
Fig. 23. Portions of two pinnules which have been bleached and stained to show the veins. S, position of a sorus; A, near the apex; B, near the base of the pinnule.

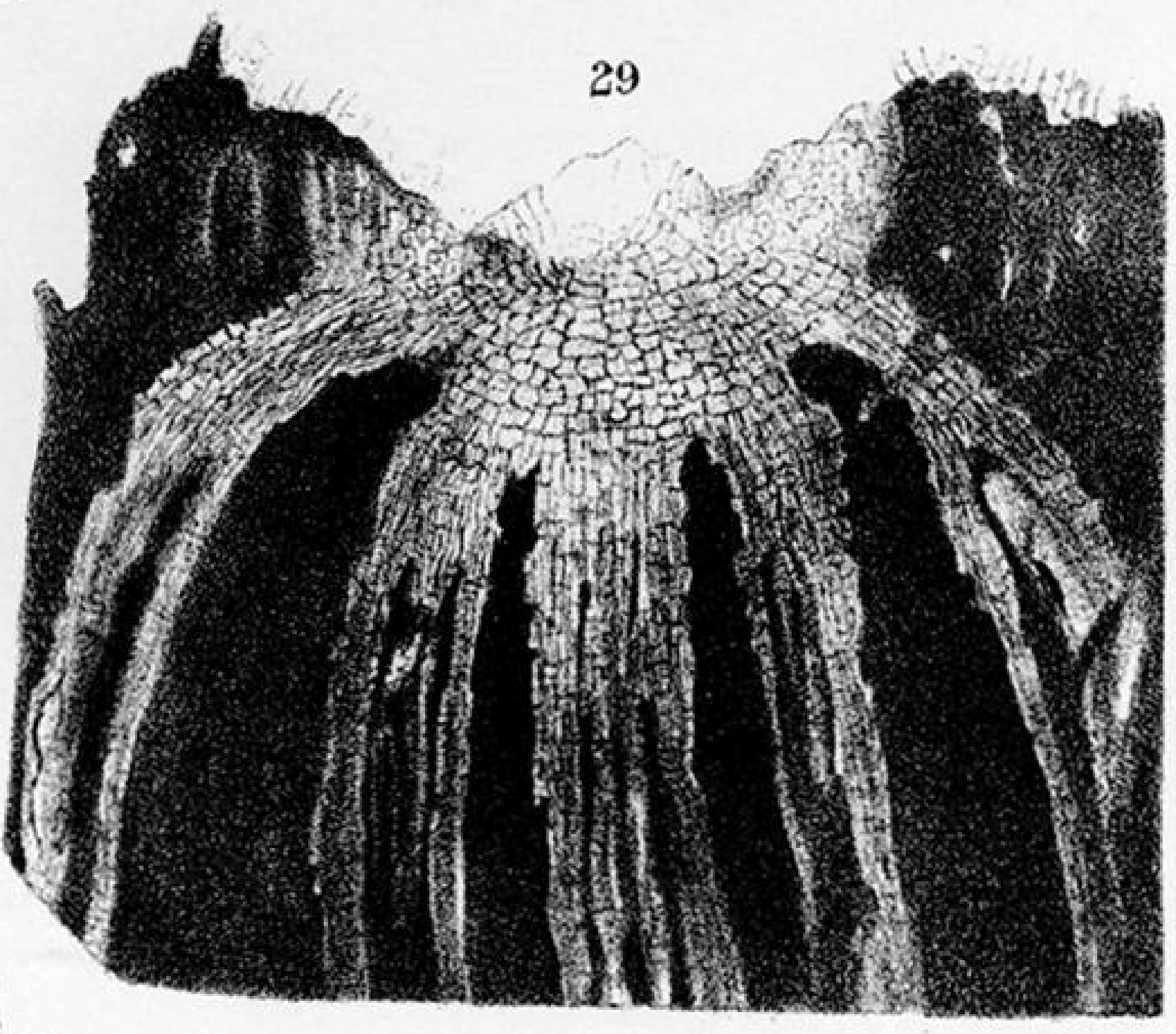


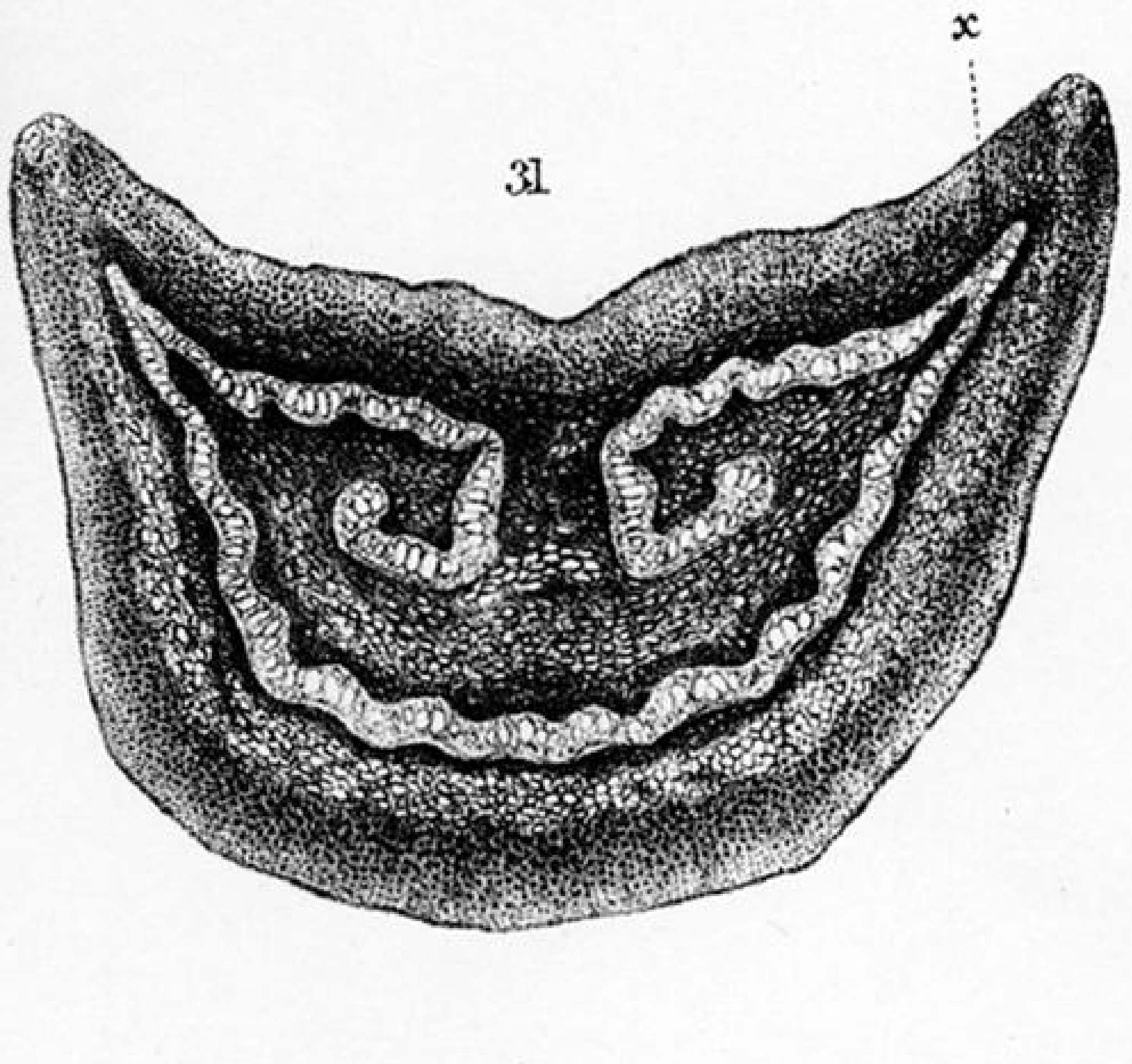












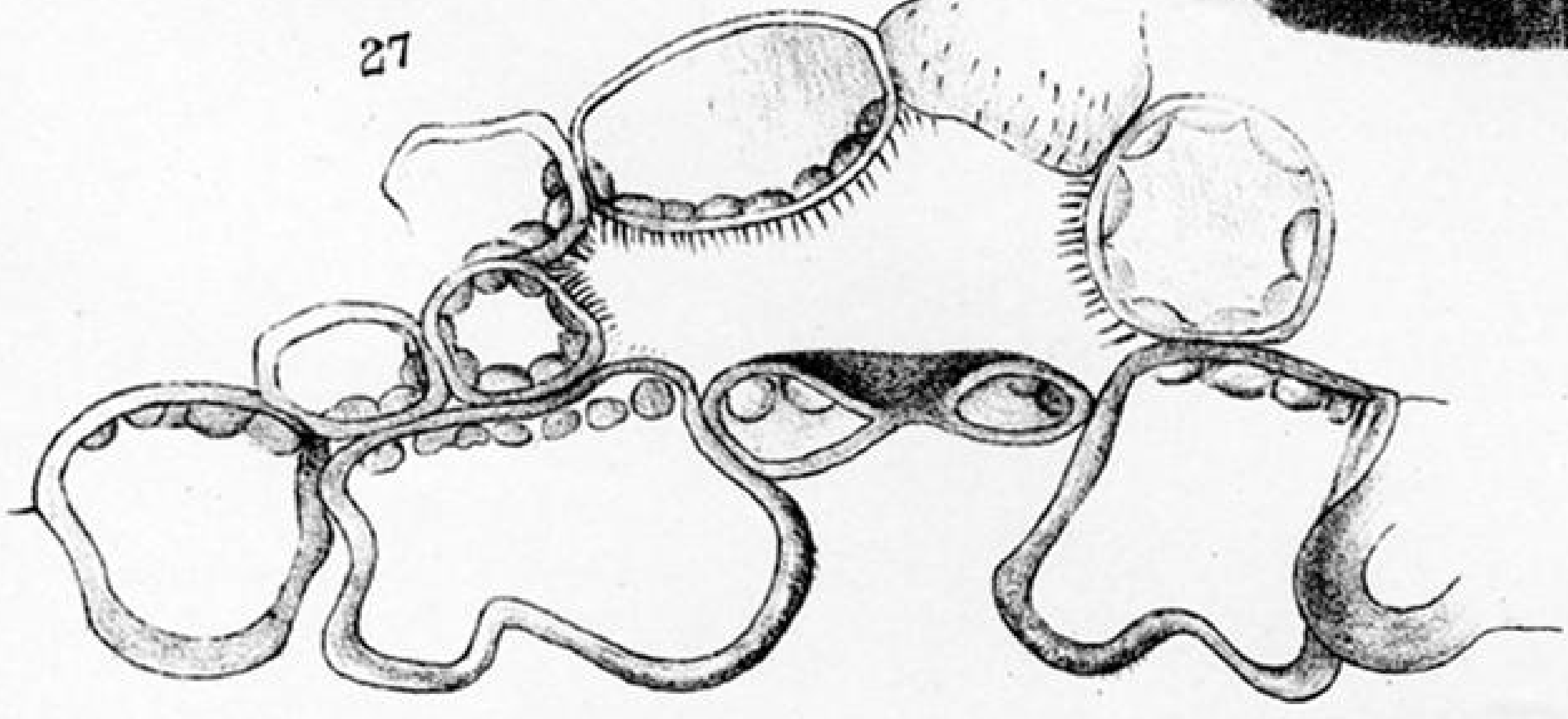


PLATE 19.

Matonia pectinata, R. Br.

Fig. 24. Transverse section of rhizome, showing the inner annular stele and the axial stele. *px*, protoxylem ; *pt.*, protophloem ; *s*, sieve-tubes ; *e*, endodermis. (× 60.)

Fig. 25. Portion of the petiole stele (*x* in the half-section of stele). P*x*, protoxylem ; *Phl*, phlœm ; E, endodermis ; P, pericycle ; *Sl*, sclerenchyma ; F, fibrous cells ; S, loose parenchyma next the protoxylem. (× 165.)

Fig. 26. Transverse section of a pinnule. (× 200.)

Fig. 27. A stoma in section ; numerous rodlets of a pectose substance projecting into the respiratory cavity. (× 325.)

Fig. 28. Transverse section of young rhizome, to show the deeply stained xylem parenchyma. *px*, single protoxylem group of inner annular stele. (× 40.)

Fig. 29. Vertical section of rhizome apex. (× 30.)

Fig. 30. Young leaf. A, in side-view ; B, in front-view ; C, transverse section through the region *a b* of B ; D, transverse stele through the region *c d* of B.

Fig. 31. Transverse section of petiole. (× 15.)

Fig. 32. Multicellular hair of rhizome. *m*, thin-walled growing cells at the base.

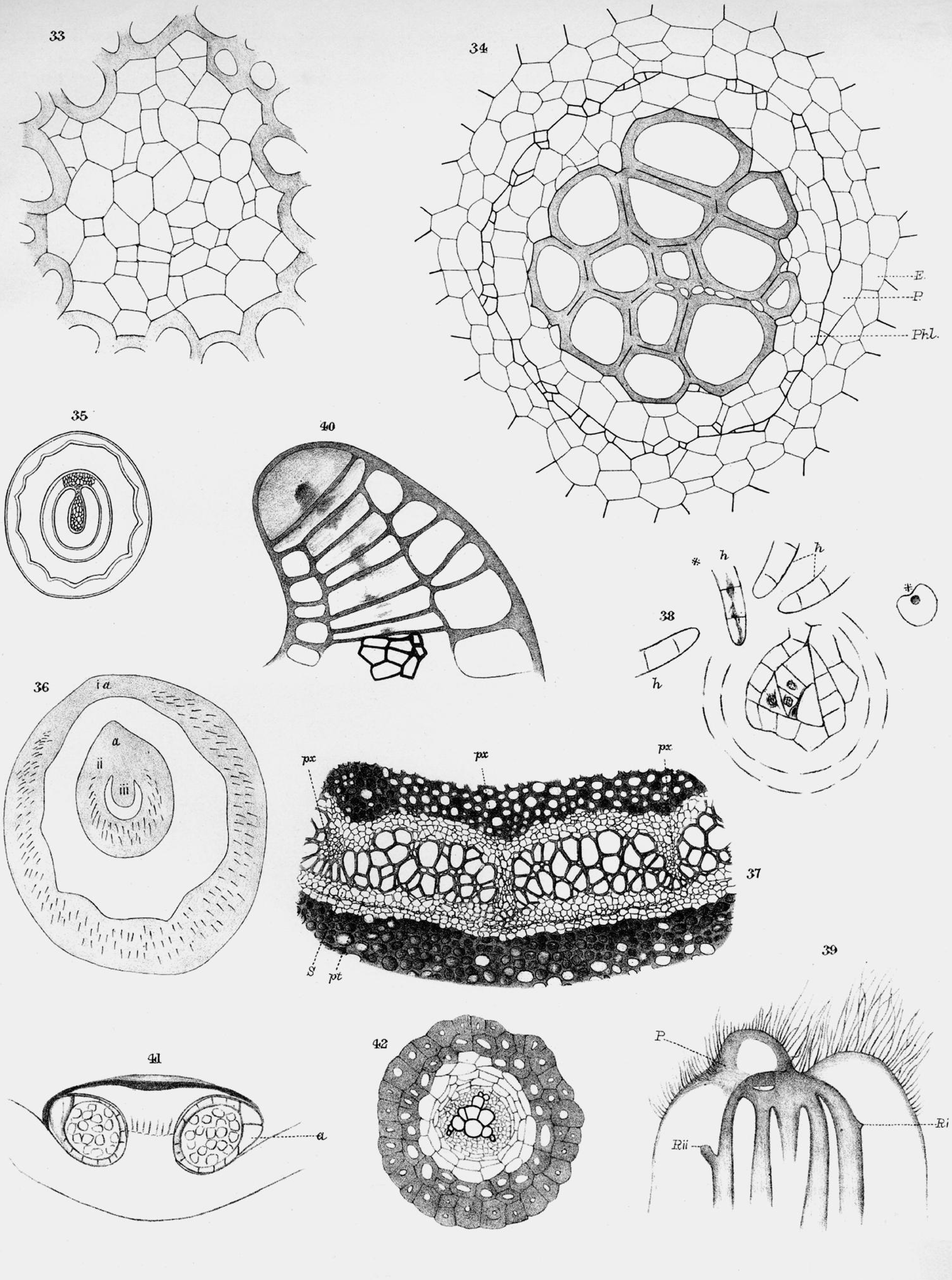


PLATE 20.

Matonia pectinata, R. Br.

Fig. 33. Transverse section of a strand of thin-walled elements (sieve-tubes, &c.) near the termination of the axial stele. (× 240.)

Fig. 34. Transverse section of the axial stele. E, endodermis; P, pericycle; *Phl*, phloem. (× 240.)

Fig. 35. Diagrammatic transverse section of rhizome, showing the axial stele continuous with the inner annular stele.

Fig. 36. Diagrammatic transverse section close to the apex of a rhizome, passing through the point of origin of the youngest leaf.

Fig. 37. Part of the outer annular stele in transverse section, showing three protoxylem groups, *px*; S, sieve-tubes; *pt*, protophloem. (× 60.)

Fig. 38. Diagrammatic transverse section through the apex of rhizome. *h*, hairs bending over the apical region.

Fig. 39. Diagrammatic vertical section of rhizome apex. *P*, position of leaf-bud; R_{i}, R_{ii}, young roots.

Fig. 40. Vertical section through the tip of a young pinnule. (× 325.)

Fig. 41. Diagrammatic vertical section of a sorus, showing two sporangia and the circular indusium. A, annulus.

Fig. 42. Transverse section of a root. (× 70.)